Interaction entre dispersion et syndromes comportementaux : causes et conséquences : approche empirique dans une population fragmentée de passereaux

Gregory Daniel

Grégory DANIEL

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Thèse dirigée en cotutelle par :

Pour l'université Lyon 1 (France) : Blandine DOLIGEZ, Chargée de Recherche au CNRS

Pour l'université d'Uppsala (Suède) : Lars Gustafsson, Professeur à l'EBC

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Ingrid AHNESJÖ (Professeur en Écologie Animale, Université d'Uppsala) - Examinateur

Dominique ALLAINE (Professeur des Universités, Université Lyon 1) – Examinateur

Thierry BOULINIER (Directeur de Recherche, CNRS) - Rapporteur

Blandine DOLIGEZ (Chargée de Recherche, CNRS) – Directrice de Thèse

Arnaud GRÉGOIRE (Maître de Conférences, Université de Montpellier) - Examinateur

Lars GUSTAFSSON (Professeur en Biologie, Université d'Uppsala) – Co-Directeur de la Thèse

Anne LOISON (Directrice de Recherche, CNRS) – Rapporteur

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Résumé

La dispersion est un trait d'histoire de vie clé pour les processus écologiques et évolutifs dans les populations naturelles. Les dernières recherches se sont notamment focalisées sur les corrélations entre traits comportementaux et la dispersion, ceci afin de mettre en évidence des syndromes comportementaux de dispersion, tout en démontrant la base génétique de la dispersion. Les dispersants ne seraient donc pas une part aléatoire d'une population, mais des individus montrant des stratégies particulières qui augmenteraient leur chances de succès.

Cette thèse s'est orientée vers trois objectifs de recherche majeurs. Le premier est la mise en évidence d'une base génétique de la probabilité de disperser dans une population fragmentée de gobe-mouches à collier *Ficedula albicollis*. Les résultats nous ont montré, au-delà de l'estimation de la base génétique de la dispersion, une distribution spatiale non aléatoire de l'apparentement dans cette population, qui pourrait être dû à des effets génétiques sur les règles de décision de choix de l'habitat. Le deuxième s'intéresse à la corrélation phénotypique et génétique entre le comportement de dispersion natale et le comportement de défense du nid, chez le martinet alpin *Tachymarpis melba*. Nous avons montré que la dispersion natale et le comportement de défense du nid sont négativement corrélés au niveau phénotypique mais aussi génétique dans ces populations. Enfin, le troisième nous à conduit à tester l'existence de syndromes comportementaux de dispersion, c'est-à-dire si les dispersants présentent un profil comportemental particulier, leur permettant en particulier de coloniser de nouveaux sites, chez le gobe-mouche à collier.

Mot-Clés : dispersion, syndromes comportementaux, héritabilité, traits de personnalité, néophobie, agressivité, prise de risque, gobemouche à collier, *Ficedulla albicollis*.

Interaction between dispersal and behavioural syndromes : causes and consequences – empirical approch in a fragmented population of passerine birds

Abstract

Dispersal is a key like history trait for ecological and evolutionary processes in wild population. The last researching particularly focused on the correlation between behavioural trait and dispersal, in order to emphasize the existence of behavioural syndromes of dispersal, and on the estimation of the genetic basis of the dispersal behaviour. Dispersant individuals could not be a random part of the population, but individuals showing particular strategies, that help them to succeed in their dispersal attempt.

This thesis has three main aims of research. The first is to show a genetic basis of the dispersal propensity in a fragmented population of collared flycatchers (*Ficedulla albicollis*). We shown not only the genetic bases of the dispersal, but also a non-random spatial distribution of relationship between individuals in this population, that might be due to genetic effects on the decision rules of habitat choice in this population. The second aim concerns phenotypic and genetic correlation between the natal dispersal and a behavioural trait, the nest-defense behaviour, in the alpin swift (*Tachymarpis melba*). We shown that natal dispersal and nest-defense behaviour are negatively correlated at a phenotypic level, but also at a genetic level in theses populations. Finally, the third aim attempt to test the existence of behavioural syndrome of dispersal, that is if dispersant individuals have a particular behavioural profile, which enable them to colonize new sites, in the collared flycatcher.

Keywords : dispersal, behavioural syndromes, heritability, personality traits, neophobia, aggressiveness, risk-taking behaviour, collared flycatcher, *Ficedulla albicollis*.

Adresses de préparation de la thèse :

En France :

Université de Lyon, F-69000, Lyon, France

Université Lyon 1, F-69622, Villeurbanne, France.

CNRS, UMR5558, Laboratoire de Biométrie et Biologie Evolutive,

F-69622, Villeurbanne, France.

En Suède :

University of Uppsala

Institutionen för ekologi och genetik, *Zooekologi*

Ekologiskt Centrum EBC, Norbyv 18 D, Norbyv 18 D

752 36 UPPSALA , Sweden

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Table des Matières

Introduction générale

La dispersion est définie comme le mouvement d'un individu depuis son site de naissance ou depuis un précédent site de reproduction vers un nouveau site de reproduction, définitions qui sont respectivement nommées dispersion natale et dispersion de reproduction (Greenwood and Harvey 1982). La dispersion est un des traits d'histoire de vie les plus importants dans les processus évolutifs, comme dans les processus écologiques, au sein des populations naturelles. La dispersion a des conséquences sur les dynamiques de population, les flux de gènes et la répartition des espèces dans l'espace et dans le temps (Clobert et al. 2001, 2009; Ronce 2007). De plus, les études sur la dispersion se rapportent de plus en plus à l'intérêt de ce phénomène en biologie de la conservation, dans un contexte de changements climatiques globaux et de dégradations locales de l'habitat (Kokko and López-Sepulcre 2006). En effet, la dispersion est l'un est principaux moyens pour les individus d'échapper aux modifications de leur environnement et aux conséquences néfastes qu'elles peuvent engendrer sur la survie et/ou la reproduction des individus. Mais que ce soit dans un but de conservation des espèces ou tout simplement pour comprendre l'impact que peut avoir ce trait dans les populations, la dispersion a suscité de nombreuses études tant théoriques qu'empiriques. Cette thèse s'inscrit dans la lignée de ce travail scientifique de compréhension du phénomène de dispersion.

La dispersion : causes ultimes et proximales

Chaque événement de dispersion se déroule en trois étapes distinctes. Tout d'abord, il y a la décision de partir du premier site, aussi appelée émigration. Ensuite, il y a le déplacement de l'individu entre deux sites, aussi nommé transfert. Et enfin, l'installation de l'individu dans un nouveau site, l'immigration (Clobert et al. 2009; Ronce 2007). Lors de chacune de ces étapes, plusieurs facteurs peuvent influencer le comportement de dispersion (Bowler and Benton 2005; Clobert et al. 2001). Classiquement sont distingués tout d'abord les facteurs ultimes, c'est à dire les facteurs induisant l'évolution de la dispersion au sein d'une métapopulation. Ils sont principalement identifiés par les modèles théoriques (revue dans Bowler & Benton 2005) ; cela peut-être les variations spatio-temporelles de l'habitat (McPeek and Holt 1992), les relations sociales entre individus d'une même espèce, ou avec des individus hétéro-spécifiques, relations pouvant être positives (coopération) ou négatives (compétition pour les ressources, prédation) ; ou encore les relations entre apparentés, comme

l'évitement de la consanguinité, ou la coopération entre individus partageant une partie de leur patrimoine génétique (Lambin et al. 2001).

Ensuite sont définis les facteurs dits proximaux. Les individus choisissent de disperser ou non en fonction de ces derniers. Les facteurs proximaux externes à l'individu définissent la dispersion contexte-dépendante. Ces facteurs proximaux sont souvent en miroir des facteurs ultimes de la dispersion. La décision d'un individu de disperser ou non peut être induite par exemple par : les facteurs abiotiques de l'environnement (Dries Bonte et al. 2008; Massot et al. 2002) ; la densité de conspécifiques, entraînant une compétition plus ou moins forte pour les ressources de l'habitat ; la pression de prédation ou parasitaire ; ou encore, dans le cas où il existe des signaux de reconnaissance entre apparentés, l'évitement des apparentés ou leur recherche en vue d'une coopération.

La dispersion a longtemps été considérée comme un trait hautement plastique, permettant à chaque individu de réagir à ces différents facteurs externes de manière optimale. Cependant, avec le nombre croissant d'études qui se sont intéressées aux capacités de dispersion des individus en fonction de leur traits propres, autrement dits internes, il est devenu évident que la dispersion est aussi phénotype-dépendante. Ces différences de dispersion liées à des traits phénotypiques peuvent être de différentes natures : morphologiques, physiologiques, comportementales et dans les traits d'histoire de vie. Par exemple, chez les insectes et les plantes, plus rarement chez les vertébrés, il a été montré que les individus dispersants peuvent présenter des morphes différents des individus non-dispersants. Ces différences peuvent être marquées, par exemple la présence d'individus ailés et d'individus aptères au sein d'une même population chez certains insectes, ou plus discrètes, par exemple une différence dans la taille du corps ou de la condition physique (Belthoff and Dufty 1998; O'Riain et al. 1996). Des différences de nature physiologique, comme, par exemple, un niveau en corticostérone (Belthoff and Dufty 1998) ou un niveau en testostérone (Holekamp 2003) plus important chez les individus dispersants, ont pu être observées. Et enfin, les individus peuvent présenter des différences comportementales liées à la dispersion, comme le comportement d'exploration, l'agressivité, l'activité des individus ou la prise de risque (revue dans Cote et al. 2010). Par exemple, les individus les plus actifs peuvent être aussi les plus dispersants (e.g. O'Riain et al. 1996 ; Belthoff & Dufty 1998 ; Bonte et al. 2004). Concernant l'agressivité, certaines études ont mis en évidence que les individus dispersants peuvent être les plus agressifs (e.g. Trefilov et al. 2000; Duckworth & Badyaev 2007), tandis que d'autres ont montré la relation inverse (e.g. Guerra & Pollack 2010) .

Parmi ces traits phénotypiques corrélés à la dispersion, les traits morphologiques ont souvent fait l'objet d'études montrant leur déterminisme génétique (Roff and Fairbairn 2001), apportant alors les premiers éléments sur la question de la base génétique de la dispersion.

La dispersion : un comportement en partie génétiquement déterminé

Pour pouvoir évoluer, un trait doit i) être variable entre individus d'une même population ou être variable entre populations, ii), avoir un impact sur la fitness des individus (survie et/ou reproduction), et enfin, iii) avoir une base génétique, c'est à dire qu'il doit présenter un certain niveau d'héritabilité.

En ce qui concerne la première condition, plusieurs études ont montré le haut niveau de variabilité de la dispersion entre individus d'une même population ou entre individus de population différentes (Matthysen et al. 2005). En ce qui concerne les travaux de recherche sur la relation entre dispersion et fitness des individus, ils n'ont pas permis de tirer de conclusions claires. Certains ont montré une relation positive entre dispersion et fitness, alors que d'autres ont conclu à une relation négative (revue dans Belichon et al. 1996). Cependant, même si le sens du lien entre dispersion et fitness n'est pas clair, il a été très fréquemment démontré. En effet, dans leur étude de 2008, Doligez & Pärt ont conclu que sur les 133 études les plus récentes de l'époque qui ont testé la différence d'un composant de la fitness entre individus dispersants et individus philopatriques, 65 ont montré l'existence d'un tel lien.

Pour tester l'existence d'une potentielle base génétique de la dispersion, différents types d'expériences ont été menées, comme la sélection de lignées sur des traits augmentant les capacités de dispersion. Ce sont des expériences qui ont été largement menées chez les invertébrés et les plantes (Roff and Fairbairn 2001). Chez les vertébrés, principalement chez les oiseaux, de telles expérience de sélection de lignées ont également été menées pour mettre en évidence la base génétique de la dispersion. D'autres études ont également été conduites sur la mise en évidence de ressemblances dans la distance de dispersion ou la propension à disperser au sein d'une fratrie (e. g. Newton & Marquiss 1983 ; Ims 1989 ; Léna et al. 1998 ; Matthysen et al. 2005 ; Sharp et al. 2008). Cependant, ces deux types d'expériences ne permettent pas d'estimer un niveau d'héritabilité de la dispersion. Les premières estimations ont été effectuées avec les régressions parents-jeunes, puis avec les modèles animaux. Les régressions parents-jeunes ont été les premières à être utilisées pour estimer l'héritabilité de la dispersion (Doligez and Pärt 2008). Néanmoins, les régressions parent-jeunes se basent uniquement sur les ressemblances dans la dispersion entre parents et jeunes. Elles n'utilisent donc qu'une partie du pedigree de la population. Les modèles animaux, quant à eux, sont des

modèles mixtes qui, grâce au pedigree entier de la population, permettent de partitionner la variance phénotypique totale d'un trait, en variance additive génétique et en variance environnementale (Kruuk 2004 ; Wilson et al. 2010). Avec de tels modèles, l'ensemble des relations d'apparentements entre individus au sein de la population est donc intégré pour estimer l'héritabilité d'un trait, et pas seulement les relations parents-jeunes. De plus, ce type d'analyse permet donc de prendre en compte la consanguinité au sein de la population. Et enfin, ces modèles permettent estimer la variance phénotypique de la dispersion, liée à d'autre facteurs, comme les effets environnementaux.

Enfin, quelques rares études ont montré un lien direct entre dispersion et gènes. Haag et al. (2005) ont fait le lien entre la fréquence allélique d'un gène codant pour une enzyme métabolique (*pgi*) et le taux métabolique en vol, tous les deux plus importants dans une population nouvellement installée et isolée de papillons, le Mélité du plantin. Trefilov et al. (2000) ont mis en relation le polymorphisme d'un codon promoteur d'un gène codant pour un transporteur de sérotonine avec l'agressivité chez le macaque rhésus. Enfin, Sinervo & Clobert (2003) ont montré que les mâles de lézards à flanc maculé présentent des comportements de dispersion différents en fonction de leur morphe de couleur, codé par le locus OBY. Il semble donc que la dispersion ait une base génétique.

Les coûts de la dispersion et les moyens de les réduire

La dispersion peut être un moyen pour les individus d'augmenter leur fitness en échappant à des contraintes environnementales réduisant leur survie ou leur reproduction dans leur habitat actuel. Cependant, c'est aussi un comportement qui génère des coûts énergétiques et des risques de mortalité importants. En effet, lors de déplacements entre sites à travers des milieux non appropriés à l'écologie de l'espèce, l'individu s'expose potentiellement à une prédation plus forte ou au manque de nourriture (Yoder et al. 2004). D'un autre côté, la sélection sur la dispersion a pu favoriser les associations entre la dispersion et des traits qui permettent de réduire les coûts associés à la dispersion, que ce soit au moment de l'émigration, du transfert ou de l'immigration. L'une des associations possibles entre dispersion et trait phénotypique serait celle avec un trait de personnalité. Le concept de trait de personnalité est relativement récent. Un trait de personnalité est défini comme des différences comportementales entre individus relativement constantes dans différents contextes et dans le temps (Gosling 2001 ; Sih et al. 2004 ; Réale et al. 2007). Par exemple, un individu qui sera plus agressif qu'un autre dans un contexte donné, restera plus agressif que ce même autre individu dans un contexte différent. Plusieurs exemples de consistances

comportementales ont été observés : pour l'agressivité (Verbeek et al. 1996), pour l'exploration (Dingemanse et al. 2002), pour la témérité (Fraser et al. 2001 ; Bize et al. 2012), pour l'activité (Sih et al. 2003), ou pour la socialité.

Traits de personnalité et dispersion

Quelques-uns de ces comportements ont été corrélés génétiquement à la dispersion. Par exemple, Duckworth & Badyaev ont montré, dans leur étude de 2007, que la colonisation d'un nouveau site de reproduction chez le merle bleu, préalablement habité par une population sœur de merle bleu, a été facilitée par l'agressivité des colonisateurs. Ils ont aussi montré qu'au cours des années qui ont suivi après la colonisation, le niveau d'agressivité avait décru dans la nouvelle population, tout en sachant que l'agressivité chez le merle bleu est un trait comportemental héritable. Un autre exemple se retrouve chez une population de mésanges charbonnières pour laquelle *Korsten et al.*, en 2013, ont montré qu'il existait un très fort lien génétique (r_G= 0,9 ± 0,40 s.e.) entre la distance de dispersion locale des individus et leur comportement d'exploration.

Ces exemples soulignent l'idée qu'il peut y avoir une intégration fonctionnelle de la dispersion avec un autre trait, ici, comportemental, se traduisant par une corrélation génétique entre dispersion et comportement. Ceci ayant pour conséquence que les dispersants ne sont pas une part aléatoire de la population, mais un sous-échantillon présentant un profil comportemental particulier de dispersion, ou syndrome comportemental de dispersion.

Les objectifs de ce travail de thèse

Cette thèse s'est orientée vers trois objectifs de recherche majeurs. Le premier objectif concerne la mise en évidence d'une base génétique de la probabilité de disperser dans une population fragmentée de gobe-mouches à collier *Ficedula albicollis*. Cette population étant suivie à long terme depuis 1980, et les individus étant individuellement identifiables par le baguage, nous avons accès à un nombre important d'événements de dispersion, qu'ils soient natals ou de reproduction, ainsi qu'à un pedigree social conséquent, nous permettant de connaître l'apparentement des individus entre eux. En utilisant des modèles mixtes de génétique quantitative (« modèle animal »), nous avons pu estimer l'héritabilité de la dispersion natale et globale (cumulant événements de dispersion natale et événements de dispersion de reproduction), ceci tout en tenant compte d'autres sources de variance, en particulier environnementales, comme la variance temporelle ou spatiale du site d'étude.

Le deuxième objectif de cette thèse est de s'intéresser à la corrélation phénotypique et génétique entre le comportement de dispersion natale et un trait comportemental, le comportement de défense du nid, chez le martinet à ventre blanc *Tachymarpis melba*. En utilisant les mêmes types de modèles animaux dans deux populations d'étude discrètes de cette espèce pour lesquelles nous disposons de données de dispersion natale et de mesures de comportement de défense du nid, nous avons estimé l'héritabilité de la dispersion natale et du comportement de défense du nid, puis testé la corrélation entre la dispersion natale et le comportement de défense du nid au niveau phénotypique mais aussi génétique dans ces populations.

Enfin, le troisième objectif consiste à tester l'existence de syndromes comportementaux de dispersion chez le gobe-mouche à collier, c'est-à-dire si les dispersants présentent un profil comportemental particulier, leur permettant en particulier de coloniser de nouveaux sites. Nous avons installé de nouveaux sites à proximité immédiate de sites déjà présents dans notre population d'étude, et mesuré les comportements d'agressivité, de néophobie et de témérité chez les individus colonisant ces nouveaux sites, lors de la colonisation puis 2 ans plus tard, une fois la population installée. Nous avons comparé les scores mesurant ces comportements chez les colonisateurs et les individus de la population déjà présente pour tester l'existence d'un profil comportemental associé à la colonisation. Nous présentons ici des analyses préliminaires.

Matériel et Méthodes

Population et site d'étude

Le travail de recherche a été mené sur une population de gobe-mouche à collier (*Fidedulla albicollis* Temm.), petit passereau (13 grammes en moyenne) appartenant à la famille des muscicapidés. C'est un oiseau migrateur vivant la saison froide en Afrique subsaharienne, et dont l'ère de répartition lors de la saison de reproduction se situe principalement de l'Est de la France à la Russie. Nous avons travaillé sur une population insulaire, séparée de l'aire principale de répartition, sur l'île suédoise de Gotland, île située au sud de la mer Baltique (57°10'N, 18°20E) (Gustafsson 1989 ; Pärt and Gustafsson 1989).

Le site d'étude, localisé au sud de l'île, est composé de forêts convenant à la reproduction du gobe-mouche à collier, principalement de chênaie-charmais, séparées par des champs et des forêts de résineux, non favorables à la reproduction de notre espèce cavicole (Gustafsson and Nilsson 1985 ; Gustafsson 1987). Nous sommes donc dans le cas d'un habitat fragmenté, dans lequel un suivi à long terme de la population a été conduit, depuis 1980, sur une quinzaine de bois (Cf. Figure 1). Dans chaque bois, des nichoirs ont été installés à environ 1,50 mètres du sol. Le modèle utilisé est facilement accepté par les gobe-mouches pour leur reproduction. Ces nichoirs sont distants de 20 mètres à 50 mètres les uns des autres. Et chaque bois comporte 20 à 150 nichoirs, en fonction de sa superficie. D'autres espèces, elles aussi cavicoles, rentrent en compétition avec le gobe-mouche à collier, pour les sites de nidification. L'occupation moyenne des nichoirs est de 40 % pour les gobe-mouches à collier, 25 % à 30 % pour les mésanges charbonnières (*Parus major*), et de 10 % à 15 % pour les mésanges bleues (*Cyanistes caeruleus)*. Ces deux espèces sont aussi compétitrices du gobe-mouche à collier en ce qui concerne l'alimentation nécessaire au nourrissage des jeunes. Le régime des jeunes est principalement composé de chenilles et autres larves. Du fait de la saturation des bois en nichoirs et du faible nombre de cavités naturelles, la quasi-totalité de la population de reproducteurs dans les bois concernés est suivie au fil des saisons de reproduction.

Suivi de la population et identification des individus.

Les mâles sont les premiers à arriver sur les sites de reproduction, aux alentours de la fin du mois d'avril, rapidement suivis des femelles. Dès les premiers signes de la présence des mâles (chants), tous les nichoirs sont visités régulièrement (tous les 2 à 3 jours) et ce, tout au long de la saison de reproduction. Ce suivi nous permet de surveiller précisément la formation

du nid, la ponte des œufs, leur éclosion, le nourrissage des jeunes, et l'envol de ces derniers. Les données de reproduction comme la date et la taille de la ponte, la condition des jeunes et leur nombre, ainsi que le nombre de jeunes prenant leur envol sont facilement obtenues grâce à ce suivi. Tous les individus naissant ou se reproduisant dans le site d'étude sont suivis individuellement tout au long de leur vie par une identification personnelle grâce à la pose de bague en aluminium (bagues fournies par le Museum d'Histoire Naturelle de Stockholm). Les jeunes sont bagués au nid lorsque ceux-ci sont âgés de 8 jours. Ils s'envolent du nid à 16-17 jours. Les parents sont capturés et identifiés lors de différentes phases de la reproduction : les femelles sont capturées dès l'incubation, tandis que les mâles sont capturés lors du nourrissage des jeunes (les femelles sont capturées de nouveau à ce moment-là). La capture à l'incubation se fait par la prise de la femelle dans le nichoir en train de couver ou par la mise en place d'un petit piège constitué de deux fils de fer barrant le trou de sortie du nichoir. Ce système de capture, léger et peu effrayant pour la femelle, ne peut être utilisé lors du nourrissage du fait de la présence des jeunes qui feraient tomber le piège. Lors de cette étape, des pièges à clapet sont utilisés. Les individus adultes capturés sont soit déjà bagués, et sont donc rapidement identifiés, soit ne le sont pas. Ces derniers sont donc des immigrants dans la population d'étude et représentent environ 35 % des adultes reproducteurs chaque année (Doligez et al. 2004). Ces individus sont alors bagués pour pouvoir les identifier par la suite.

Chaque année, une partie de la population de gobe-mouche n'est pas identifiée, 1) soit parce qu'ils sont non reproducteurs, 2) soit parce qu'ils se reproduisent dans une cavité naturelle, 3) soit parce que leur reproduction a échoué relativement tôt dans la saison, 4) soit parce que ce sont des mâles polygynes.

En effet, le gobe-mouche à collier est une espèce polygine facultative. Dans notre population, il a été estimé que 50 % des mâles vont tenter d'avoir un second territoire pour attirer une seconde femelle et parmi eux, seulement 10 % y parviennent (Gustafsson 1989). Cependant, s'ils y réussissent, ils ne s'occupent pas ou très peu de la reproduction avec la femelle secondaire, ce qui inclue le soin aux jeunes, sauf si le nid est proche ou la reproduction décalée dans le temps. En conséquence, ces mâles sont très difficiles à capturer (Doligez et al. 1999).

En plus de ce phénomène de polygynie, il a été observé un certain niveau de paternité hors couple, environ 15 % des jeunes dans 30 % des nids, ce qui est dans les limites normales trouvées chez des population de passereaux (Sheldon and Ellegren 1999).

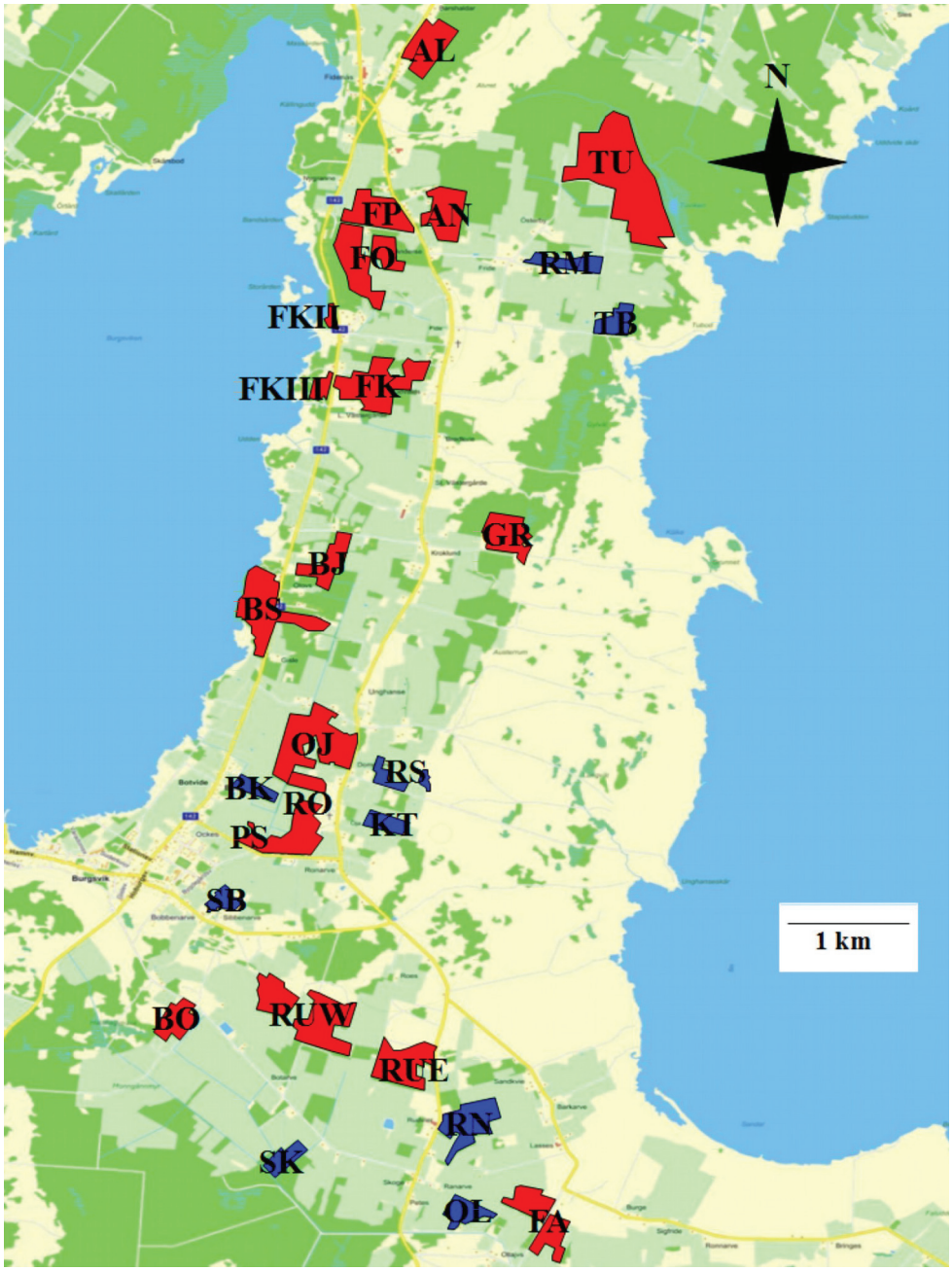

Figure 1 : Carte du site d'étude dans la partie sud de l'île de Gotland. En rouge, les 15 bois (AL, TU, AN, FP, FO,FK, GR, BJ, BS, OJ, RO,PS,BO,RUW,RUE,FA) suivis à long terme. En bleu, les 9 nouveaux bois installés en 2011 (RM, TB, BK, KT, SB, RN,OL) et en 2013 (RS, SK).

Mesures comportementales

Trois comportements ont été mesurés sur la population d'étude, entre 2011 et 2014 : l'agressivité, la néophobie et la prise de risque. Chacun des tests comportementaux se sont déroulés à des stades différents de la reproduction des couples de gobe-mouches.

L'agressivité

Les tests d'agressivité ont été effectués lors de la construction du nid, alors que les individus, et notamment les mâles, doivent défendre leur territoire contre d'éventuels compétiteurs pour ce même territoire. L'agressivité envers un conspécifique diminue après le début de l'incubation (Kral and Bicik 1989; Kral 1996; Kral et al. 1996), tandis qu'elle persiste tout au long du cycle de reproduction envers un hétérospécifique comme la mésange charbonnière (Král and Bičík 1992). Pour tester les deux types d'interactions agressives (conspécifique et hétérospécifique), deux types de leurres ont été utilisés lors des tests : des leurres de gobe-mouches ou un leurre de mésange mâle. Dans le cas des tests avec les leurres de gobe-mouches, nous avons utilisé un mâle et une femelle, afin de stimuler les deux membres du couple du nichoir. Les leurres sont des figurines d'argile grise, qui ont été peints pour imiter le plumage des oiseaux qu'ils représentent (Cf. Figure 2)

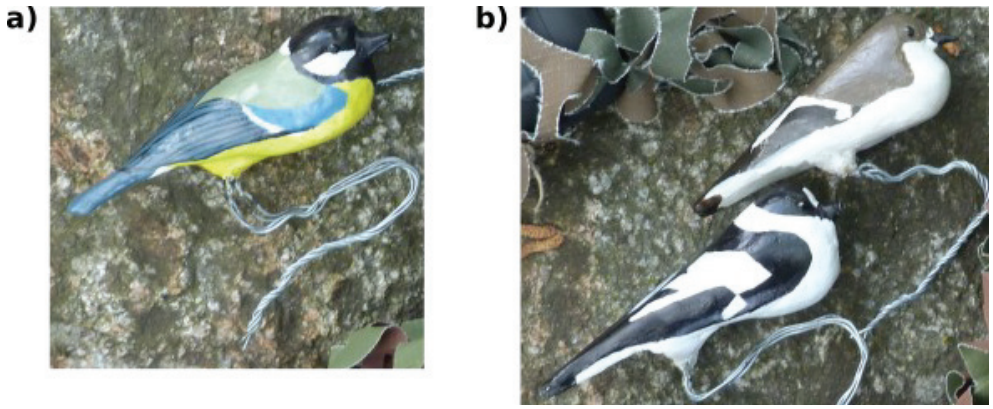

Figure 2 : Images des leurres en argile, peints, utilisés lors des tests d'agressivité : a) le leurre de mésange charbonnière mâle ; b) les leurres du couple de gobe-mouches, la femelle (au-dessus) et le mâle (en dessous).

Le leurre de mésange est installé à l'entrée du nichoir, tandis que pour les gobe-mouches, l'un des deux est installé à l'entrée du nichoir, pendant que l'autre est installé sur le toit du nichoir. Les positions de chacun (mâle/femelle) sont définies aléatoirement lors de chaque test. Au stimuli visuel est ajouté un stimuli sonore, par la mise en place d'une repasse de chant du mâle de l'espèce associée au leurre. Le dispositif audio, composé d'un petit lecteur MP3 et de petites enceintes, est camouflé sous le nichoir (Cf. Figure 3). Du fait de la nécessité de faire un grand nombre de tests sur une période de temps restreinte (jusqu'à une centaine de test par jour), cinq sets de leurres de chaque espèce ont été utilisés. Nous avons aussi utilisé cinq repasses différentes de chaque espèce. L'association leurre/chant est définie aléatoirement. La répartition des sets de leurres (un leurre mâle de gobe-mouche, un leurre femelle de gobe-mouche et un leurre mâle de mésange) est définie par bois et par jour, de telle

manière qu'un set de leurre ne soit pas utilisé deux jours de suite dans un même bois ou par un même observateur, et que chaque set de leurres passe un nombre de fois équivalent dans chaque bois.

Figure 3 : Photographies des diférents dispositifs installés sur les nichoirs lors des tests comportementaux : a) l'agressivité, avec un leurre mâle sur le toit du nichoir, un leurre femelle à l'entrée du nichoir et le dispositif de repasse de chant dissimulé sous le nichoir ; b) la prise de risque, avec un écureuil empaillé accroché à l'entrée du nichoir, et c) la néophobie, avec le nouvel objet (hockeyer) installé à droite de l'entrée du nichoir.

Un même nid est testé quatre fois durant la période de construction du nid. Le premier jour, l'espèce du leurre est déterminée aléatoirement. Le second jour, c'est l'espèce non utilisée le premier jour qui est prise pour le test. Ensuite, une journée sans test se passe afin d'éviter que l'oiseau ne se familiarise de trop avec les leurres ou le test en lui-même. Le quatrième jour et le cinquième jour, un test est de nouveau effectué et l'espèce du leurre est déterminé de la même manière que pour les deux premiers jours (Cf. Figure 4). Lors du test, l'observateur est caché sous un filet de camouflage à une distance comprise entre 5 mètres et 10 mètres du nichoir, pour une moyenne de 7 mètres environ, en fonction de la végétation présente. Le but est d'optimiser la vision de ce qui se passe au nichoir, tout en évitant d'être trop près, avec le risque que l'observateur perturbe la réaction du couple. Les différents tests effectués ont

permis de voir que l'oiseau ne repère pas l'observateur sous le filet de camouflage tant que celui-ci porte des vêtements foncés et n'élève pas la voix (à plusieurs reprises, il a pu être observé des individus de différentes espèces d'oiseaux se posant sur une branche à moins d'un mètre de l'observateur camouflé).

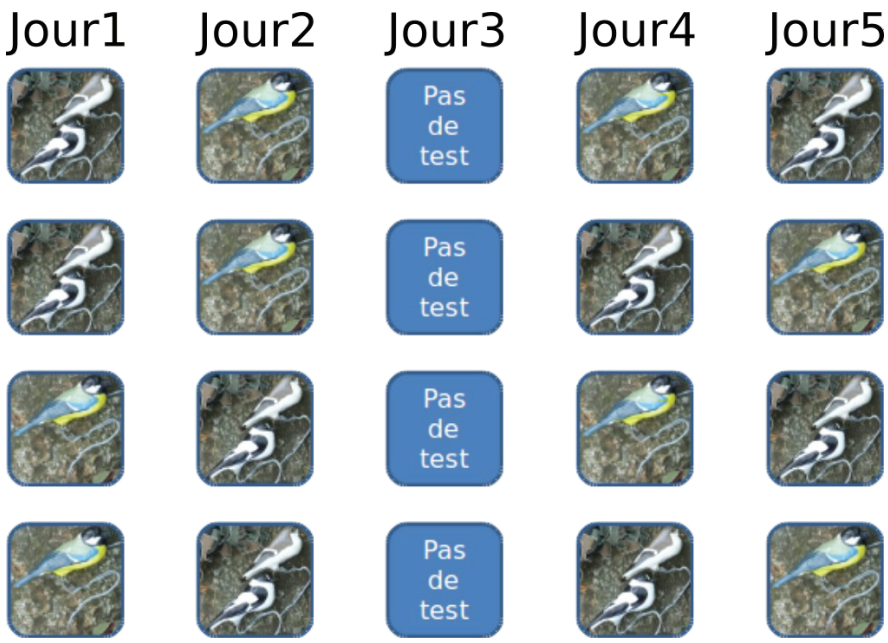

Figure 4 : Présentation des différentes combinaisons possibles de leurres utilisés (mésange ou couple de gobe-mouches) au cours du temps pour les 4 tests d'agressivité effectués sur chaque nid. Les leurres des jours 1 et 4 sont choisis aléatoirement, tandis que les leurres des jours 2 et 5 sont l'autre type de leurre, non utilisé le jour précédent.

Une phase de pré-test a été menée sur les 30 premiers nids de gobe-mouche en 2011 pour déterminer la durée optimale des tests d'agressivité à venir. Suite à ces pré-tests, la durée du test a été fixée à 15 minutes. Cela apparaissait comme un temps suffisant pour capter un maximum de réponse des oiseaux face aux leurres.

Pendant le test, l'observateur enregistre sur dictaphone : 1) chaque changement de place de chaque individu du nid (mâle et femelle), 2) la distance par rapport au nichoir où l'individu se trouve (sur le nichoir, à moins de 2 mètres, entre 2 mètres et 5 mètres, entre 5 mètres et 10 mètres, à plus de 10 mètres), 3) les alarmes des individus ainsi que leur fréquence (ponctuelle ou continue), 4) les vols stationnaires que les individus effectuent au-dessus du nichoir ou des leurres, 5) les attaques directes sur un leurre, en rase-motte ou en attaque physique frontale (coup de bec), 6) la présence d'autres individus (gobe-mouches, mésanges

ou autres espèces), qui pourrait influencer le comportement des individus du nid. A la fin du test, l'observateur range son matériel, retire le ou les leurres, ainsi que le dispositif audio du nichoir et s'en éloigne rapidement afin de perturber le moins possible les oiseaux par une présence humaine visible.

La néophobie

Le test de néophobie se déroule au moment du nourrissage des jeunes, quand ceux-ci sont âgés de 5 jours. A cette période, la demande des jeunes en nourriture étant la plus forte, les parents doivent s'investir au maximum dans le nourrissage des jeunes. La néophobie n'est testée qu'une seule fois par nid, et le comportement est enregistré par une caméra vidéo. Tester la néophobie des individus revient à tester leur peur d'un nouvel objet dans un environnement connu (Garamszegi et al. 2009 ; Greenberg and Mettke-Hofmann 2001 ; Mettke-Hofmann et al. 2002). Ici nous avons utilisé une petite figurine de hockeyeur bleue et rouge, d'environ 7 cm de hauteur (Cf. figure 3). Du fait que le nourrissage peut varier entre individus et que la réponse au nouvel objet peut varier différemment entre individus, le test se déroule en deux phases. Lors de la première phase, nous enregistrons le comportement normal des individus du nid, sans le nouvel objet. Cette phase nous servira de base de comparaison avec la seconde phase du test. Lors de la seconde phase, l'objet est installé. Cela nous permet donc de voir la réaction des individus par rapport à ce nouvel objet. La caméra est installée le plus loin possible du nichoir tout en optimisant la qualité de l'image, entre 6 m et 10 m du nichoir généralement. Le cadrage de la caméra est resserré sur le nichoir, ce dernier occupant les deux-tiers de l'image, afin de pouvoir différencier avec certitude le mâle (noir et blanc) de la femelle (marron-brun). L'observateur débute l'enregistrement, puis il simule la mise en place de la figurine sur le nichoir afin de standardiser le temps passé au nichoir entre la phase 1 et la phase 2 du test. Enfin il s'éloigne rapidement du nichoir (plus de 100 mètres). Une fois l'heure passée, l'observateur revient, contrôle la caméra (charge de la batterie, modification éventuelle du cadrage), fait les ajustements nécessaires, puis punaise la figurine pour qu'elle se positionne juste à droite de l'entrée du nichoir. Il repart pendant une heure, puis revient pour arrêter l'enregistrement et retirer la figurine et le matériel d'enregistrement.

Lors du visionnage de cet enregistrement vidéo, les comportements relevés sont, pour chacune des phases : 1) le temps de retour de chacun des individus au nichoir, 2) le nombre d'entrées dans le nichoir, 3) le nombre de vols stationnaires au-dessus de la figurine ou du nichoir, et enfin, 4) le nombre d'attaques sur l'objet.

La prise de risque

Ce test se déroule lorsque les jeunes sont presque prêts à l'envol, quand ils sont âgés de 13 et 14 jours. A ce stade avancé de la reproduction, les parents ont beaucoup à perdre dans l'échec de leur reproduction. En effet, ils ont déjà beaucoup investi dans l'élevage des jeunes. La prise de risque des individus est observée dans un contexte de défense du nid avec la présence d'un prédateur de nid sur le nichoir.

Pour simuler la présence d'un prédateur de nid, un écureuil ou un pic épeiche empaillé a été fixé au trou d'entrée du nichoir (Cf. Figure 3). Nous avons utilisé deux exemplaires de chaque espèce de prédateur. L'espèce et le numéro du leurre utilisé pour chaque test était déterminé par bois et par jour, de telle sorte que chaque leurre soit utilisé un nombre de fois équivalent dans chaque bois et que chaque leurre ne soit pas utilisé deux jours de suite dans le même bois. En procédant ainsi, nous cherchions non seulement à minimiser la probabilité que les individus d'un même bois s'habituent à un leurre en particulier, mais aussi à randomiser l'utilisation des leurres au sein de chaque bois. Enfin, si un leurre d'écureuil a été utilisé le premier jour de test, alors un leurre de pic épeiche a été utilisé pour le second jour de test, et inversement.

Les pics épeiches empaillés ayant été trop dégradés lors de la première année, ils ont été retirés des tests lors des années suivantes et remplacés par 3 nouveaux écureuils empaillés. Ainsi, après 2011, les tests de prises de risques se sont uniquement effectués avec des écureuils empaillés, dont la répartition par bois et par jour a suivi le même processus de randomisation qu'en 2011 avec les écureuil et les pics épeiches.

Les tests préliminaires effectués en 2011 pour les 20 premiers nids rendu à ce stade dans notre population, duraient initialement 15 minutes. Nous avons eu de vives réactions des oiseaux, très rapidement après que l'observateur se soit caché sous le filet de camouflage (parfois dans les secondes qui suivirent). En conséquence de quoi, le test a été réduit à une durée de 5 minutes à partir du moment où les individus des 2 sexes sont présents, pour une durée maximale n'excédant pas 10 minutes. Faire durer le test plus longtemps peut être traumatisant pour le ou les parents présents, de même que pour les poussins dans le nid (observations personnelles). Pour éviter toute sorties prématurées des jeunes du nid pendant le test, l'entrée du nichoir était obstruée. Cependant, en 2012, l'année fut très bonne pour la reproduction du gobe-mouche. Les jeunes âgés de 13 jours étaient plus avancés dans leur développement qu'à l'habitude. Et nous avons pu observer quelques diminutions de nichées entre le premier et le second test, supposant le départ du nid de certains jeunes. Suite à cela, et parce que des tests préliminaires sur les données de l'année précédente ont montré que le

comportement des individus était répétable entre les deux tests, il a été décidé de ne faire plus qu'un seul test par nichoir, afin d'éviter tout départ précoce des jeunes du nid.

Les comportements sont enregistrés sur dictaphone, par observation directe des oiseaux, sous un filet de camouflage, à une distance du nichoir allant de cinq mètres à dix mètres en fonction de la végétation aux alentours. L'observateur commence par préparer son matériel afin de pouvoir démarrer le test le plus rapidement possible après la pose du leurre sur le nichoir. Une fois la pose faite et le retour sous le filet de camouflage, le test commence. Différents comportements sont enregistrés par l'observateur : 1) les distances de l'individu par rapport au nichoir (sur le nichoir, à moins de 2 mètres, entre 2 mètres et 5 mètres, entre 5 mètres et 10 mètres, à plus de 10 mètres), 2) les déplacements de l'individu, 3) les vols stationnaires au-dessus du leurre, et 4) les attaques à coups de bec ou en rase-motte sur le leurre.

A la fin du test, l'observateur range le plus rapidement possible son matériel, ainsi que le leurre, puis quitte la zone du nichoir, en évitant de faire des tests successifs sur 2 nichoirs distants de moins de 50 mètres.

L'expérience de colonisation

Afin de tester l'hypothèse de la présence d'un profil comportemental de colonisateur au sein notre population, nous avons mis en place une expérience de colonisation. Au tout début de la saison de reproduction, nous avons installés de nouveaux nichoirs dans des bois qui en étaient dépourvus jusqu'ici. Ces nouveaux bois sont à proximité (moins d'un kilomètre) des bois suivis à long terme. Les nichoirs installés sont de même type que ceux dans les bois suivis à long terme. De même, ils ont été fixés à la même densité et à la même hauteur que dans les bois suivis à long terme. Le panel de nouveaux bois présente des caractéristiques environnementales (densité d'arbres, espèces d'arbre présentes) similaires à celles des bois suivi à long terme, avec un mélange de bois de forte densité arbustive, et d'autres plus ouverts (*änge*).

En 2011, huit nouveaux bois ont été installés (Cf. Figure 1). A la fin de la saison de reproduction, dans un des nouveaux bois, il est apparu que le nombre important de gobe-mouches présents dans le bois tout au long de la reproduction (repérés visuellement ou par les alarmes et les chants) ne reflétait pas le nombre de couples installés dans les nichoirs. Le bois présentant une quantité plus importante de vieux arbres, nous en avons déduit qu'il offrait un nombre important de cavités naturelles pour la reproduction du gobe-mouche. Il a donc été

désinstallé à la fin de la saison de reproduction et les tests effectués sur les couples de gobe-mouches présents dans ce bois ont été écartés des analyses. En 2012, pour augmenter notre taille d'échantillon, trois nouveaux bois ont été installés. Dans l'un de ceux-ci, aucun couple de gobe-mouches ne s'est reproduit. Il a donc été écarté des analyses. Au final, entre 2011 et 2012, neuf nouveaux bois, contenant 20 à 60 nichoirs chacun, ont été installés et retenus pour notre expérience. La population de gobe-mouches dans ces bois a été suivie de la même manière et a subie les même tests comportementaux que la population de gobe-mouches présente dans les bois suivis à long terme.

Les nichoirs ont été installés avant l'arrivée des gobe-mouches. Lors de la pose, l'entrée de tous les nichoirs a été obstruée afin d'éviter que des couples de mésanges s'installent dans les nichoirs, fournissant alors une information sociale sur le bois aux gobe-mouches à collier arrivant, et réduisant le nombre de nichoirs disponibles à la colonisation par des couples de gobe-mouches. Dans les deux jours qui ont suivi les signes de l'arrivée des premiers gobe-mouches sur le site de reproduction (par observation directe ou en entendant le chant des mâles), les nichoirs ont été désobstrués.

Étude sur une population de martinets à ventre blanc : présentation succincte du site d'étude et de l'espèce

L'étude du second chapitre s'est déroulée sur une population suisse de martinet à ventre blanc (*Tachymarptis melba* L.), en collaboration étroite avec Pierre Bize de l'université d'Aberdeen (Royaume-Uni) qui gérait le suivi de cette population durant les années pendant lesquelles les données ont été récoltées. Nous allons succinctement vous présenter la population et le site d'étude, ainsi que la mesure de défense du nid. Vous pourrez trouver un complément d'information dans le chapitre 2 de cette thèse et dans les publications citées.

Le martinet à ventre blanc est un oiseau migrateur nichant en colonie sur les parois rocheuses ou dans des bâtiments élevés. Lors de la saison de reproduction, son aire de répartition_ est limitée à l'espace méridionale de l'Europe et au Sud-Ouest de l'Asie. Les martinets adultes retournent dans leurs précédents sites de reproduction et ne font qu'une seule ponte par an de 1 à 4 œufs (Bize et al. 2006, 2012). Ce sont des oiseaux monogames et l'investissement parental dans la reproduction est le même pour le mâle et la femelle. Les jeunes sont sexuellement matures à l'âge de 2 ou 3 ans (Tettamanti et al. 2012) et se reproduisent pour la première fois majoritairement dans leur site de naissance.

La population d'étude est en Suisse, répartie en deux colonies distantes l'une de l'autre de 21 km dans les tours horloge de Bienne (47°10’N, 7°12’E) et de Solothurn (47°12’N, 7°32’E), avec environ 100 et 50 couples nicheurs par an, respectivement. Un suivi régulier de la reproduction est effectué chaque année. Les parents sont capturés à l'incubation ou au nourrissage des jeunes, identifiés individuellement par une bague numérotée, mesurés, et bagués s'ils ne l'étaient pas. Les jeunes sont bagués au nid à l'âge de 10 jours.

La dispersion natale des jeunes est déterminée de façon binaire, c'est à dire que les individus bagués au nid dans une colonie, se reproduisant pour la première fois dans cette même colonie sont déterminés comme non-dispersants ou philopatriques. Inversement, les individus qui ne se reproduisent pas dans la même colonie que leur colonie de naissance sont déterminés comme dispersants. Du fait que tous les individus adultes sont philopatriques dans notre population, les immigrants non bagués dans les 2 colonies sont considérés comme des dispersants pour la dispersion natale dans les analyses.

Entre 2013 et 2014, lors de la capture des adultes, le comportement de défense du nid des individus reproducteurs a été mesuré par un seul observateur suivant un gradient timidité-témérité de 5 niveaux, allant de 0 à 2, avec un pas de 0,5. Cette mesure se rapporte à la réaction des individus face à l'approche d'un humain et de la capture à la main (Bize et al. 2012; Patrick et al. 2013). Les individus s'envolant du nid dès la détection de l'observateur se voient assigner le score le plus bas (0), tandis que les individus qui, à l'approche de l'observateur, vont vers lui, battent des ailes et griffent la main se voient affectés le score le plus haut (2) (détails dans le chapitre 2 et dans Bize et al. 2012).

CHAPITRE 1

Heritability of between-patch dispersal propensity in a passerine bird: a role for individual habitat selection rules?

Grégory DANIEL[1,2], Lars GUSTAFSSON[2] and Blandine DOLIGEZ[1,*]

In prep.

Heritability of between-patch dispersal propensity in a passerine bird: a role for individual habitat selection rules?

Grégory DANIEL[1,2], Lars GUSTAFSSON[2] and Blandine DOLIGEZ[1,*]

[1] CNRS, Department of Biometry and Evolutionary Biology, UMR 5558, Université de Lyon, Université Lyon 1, 43 boulevard du 11 novembre 1918, Bâtiment Gregor Mendel, 69622 Villeurbanne cedex, France

[2] Animal Ecology, Department of Ecology and Genetics, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18d, 75236 Uppsala, Sweden

* Corresponding author

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Running head

Heritability of dispersal propensity

Abstract

Although dispersal has long been considered as a plastic trait affected by both environmental factors and individual condition, recent studies have revealed a genetic basis of dispersal behaviour in various taxa, with moderate estimates of dispersal heritability. However, heritability estimates are not fixed and can be strongly affected by environmental variation. Nevertheless, none of the previous studies estimating dispersal heritability in the wild specifically investigated the influence of accounting for environmental variation on heritability estimates. Here, using animal (mixed) models, we tested whether and to which extent heritability estimates of between-patch dispersal propensity were affected when different sources of variance (i.e. different random factors) were accounted for, in a patchy population of collared flycatchers Ficedula albicollis. When the models included no other source of variance than additive genetic variance, we found a moderate heritability estimate for natal dispersal, which confirmed previous results in this population. The heritability estimate for global dispersal (i.e. including both natal and breeding dispersal) was lower, probably due to the influence of personal experience (e.g. personal reproductive success) in dispersal propensity in adults. We explored the influence of spatial (patch) and temporal (year) environmental variance, as well as maternal identity. Year and maternal identity had little impact on dispersal heritability estimates. Conversely, including patch as a random effect yielded a strong decrease in heritability estimates for both natal and global dispersal, showing that spatial (patch) variance captured part of the additive genetic variance rather than residual, unexplained, variance. Including measures of local habitat quality (i.e. local breeding density and reproductive success) did not allow modelling this spatial environmental variance, even though dispersal propensity decreased with increasing local habitat quality. These results suggest that genetic relatedness between individuals was spatially structured in the study population, such that related individuals were more likely to be found in the same patches. This was confirmed by a significant but weak correlation between the relatedness and spatial similarity matrices. Such a spatial structure was unlikely to result from limited dispersal movements in this species, but could be due to heritable habitat selection rules, leading related individuals to settle in the same patches. Future work is needed to investigate the genetic basis of habitat selection rules, in particular via information use.

Introduction

Dispersal, defined as the movement from the birth site or previous breeding site to a new breeding site (natal and breeding dispersal respectively; (Greenwood and Harvey 1982), is a key life history trait for many ecological and evolutionary processes, as well as for conservation in the wild (Clobert et al. 2001, 2012; Edelaar and Bolnick 2012; Kokko and López-Sepulcre 2006; Ronce 2007). Dispersal has long been considered mainly as a plastic behaviour allowing individuals to adjust decisions to local conditions, and in particular to escape degrading environmental conditions (Clobert et al. 2001). Accordingly, dispersal decisions have been shown to be triggered by many external factors encompassing ecological (temporal and spatial habitat heterogeneity, environmental stochasticity; e.g. McPeek and Holt 1992), social (positive and negative interactions with kin and non-kin; e.g. Lambin et al. 2001) and/or genetic (inbreeding/outbreeding avoidance, kin cooperation or competition; e.g. Lambin et al. 2001; Le Galliard et al. 2003) variation in the environment (Bowler and Benton 2005; Clobert et al. 2004). Individuals' decision to disperse can also be partly determined by internal factors that depend on environmental factors (e.g. body condition; (Clobert et al. 2009; O'Riain et al. 1996). Although many empirical studies have helped circumscribe the proximate causes of dispersal, the evolutionary potential of this trait has mainly been addressed in theoretical studies and remains largely unknown in most populations, with some noteworthy exceptions (e.g. (Duckworth and Badyaev 2007; Phillips et al. 2006; Schtickzelle et al. 2006; Thomas et al. 2001).

A trait evolves in response to evolutionary pressures if three conditions are met: (i) the trait must show between-individual variability, within and/or among populations; (ii) the trait must be linked to individual fitness, even if this link varies in space and time, and (iii) the trait must have a genetic basis, i.e. be at least partly heritable (Roff and Fairbairn 2001). Regarding the first condition, dispersal is often highly variable between individuals, in terms of propensity, distance and/or direction (e.g. Bowler and Benton 2009; Matthysen et al. 2005; Winkler et al. 2005). Regarding the second condition, although general patterns of associations between dispersal and fitness components are unclear, many studies report fitness differences between dispersing and non-dispersing individuals (reviews in Belichon et al. 1996; Doligez and Pärt 2008) . Finally, regarding the third condition, although the plasticity of dispersal has been acknowledged, morphological, behavioural and physiological traits that strongly affect dispersal capacity have been shown to be heritable in plants and invertebrates (Cheptou et al. 2008; Friedenberg 2003; Roff and Fairbairn 2001; Saastamoinen 2008). Direct

measures of dispersal in the wild were however rarely analysed as such in these organisms, mostly because of the difficulty to monitor individuals in natural populations. Rather, dispersal-related traits such as seed or wing morphology, overall activity and flight capacity were used to measure dispersal in these studies (Roff and Fairbairn 2001). One study also reported direct genetic variation associated to dispersal in a butterfly species (Haag et al. 2005). In vertebrates, evidence for a genetic basis of dispersal remains limited so far. Direct links between genetic variation and dispersal behaviour come from only two studies (Sinervo and Clobert 2003; Trefilov et al. 2000). A number of studies have estimated the heritability level of dispersal propensity or distance, most often using parent-offspring regressions (e.g. (Doligez et al. 2009; Sharp et al. 2008); review in (Doligez and Pärt 2008) and in a smaller number of cases using quantitative genetics mixed models called 'animal models' that estimate the fraction of total observed phenotypic variance of a trait in a population due to additive genetic variance by using information about the degree of relatedness between individuals obtained from their pedigree (Charmantier et al. 2011; Doligez et al. 2012; Duckworth and Kruuk 2009; Korsten et al. 2013; McCleery et al. 2004).

Animal models are more powerful than parent-offspring regressions in tearing apart variance linked to genetic effects from environmental effects shared by related individuals and thus estimating heritability because (i) they derive information from all relationships between individuals, thereby maximizing statistical power, (ii) they are more robust to unbalanced sampling designs, inbreeding and selection effects and (iii) they can account for other sources of phenotypic variance (Charmantier et al. 2014; de Villemereuil et al. 2013; Kruuk 2004; Wilson et al. 2010). The last point may be critical, because selection experiments under controlled conditions have shown that dispersal heritability estimates may strongly depend on environmental conditions (e.g. Bitume et al. 2011; see also for on life-history traits: Laugen et al. 2005; for body condition: Crespel et al. 2013). A comprehensive understanding of the genetic basis of dispersal may therefore require accounting for spatio-temporal variation in environmental conditions and assessing the extent to which such variation affects heritability estimates in the wild. Yet, only two previous animal model studies on dispersal heritability investigated environmental sources of variance besides the additive genetic variance (Korsten et al. 2013; McCleery et al. 2004) while other studies ignored such sources of variance or included them as fixed effects in the model (e.g. cohort in (Duckworth and Kruuk 2009); natal colony in (Charmantier et al. 2011), which does not allow estimating their importance relative to additive genetic variance. When year and plot of birth were included in the model, the variance directly associated to these effects was small (Korsten et al. 2013; McCleery et al.

2004). In the Korsten et al. study (2013), however, important variance was associated with natal brood, which includes effects linked to the natal environment in general (parental effects as well as spatio-temporal variation in rearing conditions). Because this study did not compare heritability estimates obtained with and without accounting for natal conditions, it is however not possible to assess whether this source of variation influenced heritability estimates.

Here, we assessed whether and how accounting for environmental sources of variation affected heritability estimates of dispersal propensity in a patchy population of collared flycatchers (*Ficedula albicollis*). Using animal models, we estimated dispersal heritability in absence and presence of spatial (patch) and temporal (year) environmental random effects, as well as maternal identity. We also tested whether spatio-temporal variance could be modelled via measures of local habitat quality previously found to affect dispersal decisions in this species (patch density and reproductive success of conspecifics in a given year; (Doligez et al. 2002, 2004). By comparing these models, we assessed the relative importance of each source of variance on dispersal and how their estimate may depend on each other. While we expected environmental variation to account more specifically for part of the residual variance, it could also affect the estimate of the additive genetic variance if the population shows a spatio-temporal structure in relatedness between individuals due to dispersal patterns.

Material and Methods

Study area and study population, pedigree data

The study population of collared flycatchers is located in the southern part of the Swedish island of Gotland (57°10' N, 18°20' E). Breeding flycatchers have been monitored in this population since 1980 (Part and Gustafsson 1989), but because new breeding patches were settled until 1986 and because experiments affecting dispersal were conducted from 2005 onwards, we used here dispersal data collected between 1988 and 2005.

Collared flycatchers are small migratory hole-nesting passerine birds that readily breed in artificial nest boxes, providing easy access to breeding data and young, as well as adult identity. Nest boxes have been visited regularly each year over the 14 spatially discrete study forest patches, which are separated by unsuitable habitat for breeding in this species, to record breeding data. Adults breeding in nest boxes have been caught inside boxes (females during incubation and males during nestling feeding), identified and ringed if previously unringed

(i.e. immigrants into the study site) and all offspring have been ringed. Thus, individuals are monitored throughout their lives within the study site, providing data on their natal and dispersal events and a social pedigree of the population (Table 1). More detail on the study population, study site and monitoring procedures can be found in Gustafsson (1989), Part and Gustafsson (1989), Doligez et al. (2004), Doligez et al. (2009) and Doligez et al. (2012).

The ability to obtain precise heritability estimates from animal models depends on the quality of the available pedigree data. In the study population, pedigree quality could be affected by (i) missing information for adults that were not captured, (ii) missing relatedness links due to immigration in and emigration out of the study area and (iii) extra-pair paternity. Adult capture probability was here tightly linked to reproductive activity and success. Consequently, non-breeders and early failed breeders (during laying for females, before nestling mid-rearing period for males) remained most of the time unidentified. Because these individuals produced no offspring and because the capture rate of successful breeders was very close to 1, these non-captures did not strongly affect the knowledge of relatedness between individuals in the pedigree; yet, they may bias observed dispersal events (see below). The collared flycatcher is a facultatively polygynous species, with an estimated 10% of males attracting a second female each year but providing little care to their secondary brood (Gustafsson 1989). As a result of this reduced brood attendance, polygygnous males were less likely to be caught. However, secondary broods usually suffer from increased mortality, thus these missed males should again not strongly affect the pedigree. Each year, approximately 40% of adult breeders were unringed in the study area, corresponding to a mix of immigrants and previously missed local birds. The arrival of new birds in the pedigree should reduce the length of relatedness connections between individuals. Furthermore, temporary emigration outside of the study area (Doligez et al. 2004) may also generate missing links between related individuals but quantifying this effect is challenging in spatially limited study sites. Finally, the level of extra-pair paternity in this population was found to be within the average range in small passerine populations (i.e. 15% of extra-pair nestlings in 30% of nests; Sheldon and Ellegren 1999). Extra-pair paternity should therefore not strongly affect our heritability estimates (Charmantier and Réale 2005).

Definition of dispersal status and dataset

In this study, dispersal was defined as a change of breeding patch either between the year of birth and the first breeding attempt (natal dispersal) or between two successive breeding attempts (breeding dispersal). Dispersers were individuals that changed patch and philopatric

individuals were those that remained in their previous patch, i.e. we used a binary definition of dispersal (Doligez et al. 1999, 2004, 2012). This binary definition has previously been shown to be biologically relevant in this population (e.g. Doligez et al. 2002, 2004, 2009; Doncaster et al. 1997) and allowed us to avoid methodological constraints linked with dispersal distances in a fragmented and spatially limited study site (Doligez et al. 1999; van Noordwijk 1984). A fraction of adults cannot be captured each year (see above), which may bias the distribution of observed dispersal events if dispersal is linked to reproductive activity and/or success. Directly testing for differences between dispersing and philopatric individuals in the probability to skip breeding and/or early failure probability is challenging, because it would require obtaining information from these uncaught individuals. However, recent evidence showed that dispersing and philopatric individuals do not differ in lifetime reproductive success in this population except when conditions degrade unexpectedly (Germain et al. submitted). This suggests no strong difference in the probability to breed successfully depending on previous dispersal status (see also Doligez et al. 2004). Furthermore, a third of individuals in any given year were subsequently recaptured after one or more years of delay (Doligez et al. 2009). This may have resulted in misclassifying dispersal status if individuals changed patch during the year when they were missed. A detailed discussion about the impact of such misclassification was provided in Doligez et al. (2012).

Because natal and breeding dispersal are frequently under different selective pressures (Greenwood and Harvey 1982), we estimated the heritability of natal dispersal events alone and then all dispersal events (i.e. natal and breeding dispersal) separately. Over the 18 years of the study, we recorded 3,013 natal dispersal and 2,093 breeding dispersal events of individuals with known parents (out of 6,571 individuals in total). Although many of the previously unringed individuals were probably dispersers from out of the study area, their dispersal status was considered unknown to analyse only individuals whose dispersal status was determined with certainty. Many cross-fostering experiments have been performed in the study areas over years to investigate various research questions. All cross-fostered individuals were discarded from the analysis. The statistics of the pedigree for individuals informative to our analyses are summarized in Table 1.

Animal model analyses

Using relatedness information from the social pedigree information and phenotypic data on individual dispersal status, we partitioned the total phenotypic variance in dispersal (V_P) into

additive genetic (V_A), patch (V_{Patch}), year (V_{Year}), maternal identity (V_{Mat}) and residual components (random effects). Patch and year were included to account for spatial and temporal variation in dispersal propensity, respectively. Maternal identity was included to account for maternal influence on dispersal propensity, found in various taxa (e.g. Meylan et al. 2002; Sinervo et al. 2006; Tschirren et al. 2007). For the analysis of all dispersal events (global dispersal), several breeding dispersal records could be recorded for each individual (mean number of observations per individual: 1.6; minimum: 1; maximum: 8). We therefore added individual identity as a random effect (V_I) to account for permanent environment effects, i.e. differences between individuals not already attributed to additive genetic variance (Wilson et al. 2010). Additive genetic and, for global dispersal, individual effects were included in all models. To investigate the impact of accounting for different sources of environmental variation on heritability estimates, we included additional random effects (patch, year, maternal identity) either separately or in combination with each other, including a patch × year interaction (i.e. 10 different models in each case; Figure 1). Because individuals may make dispersal decisions based on environmental cues gathered both in the previous and current year (e.g. Kivelä et al. 2014), we first explored the effects of departure patch and year, and second of arrival patch and year. Dispersal heritability estimates did however not differ between models including one or the other effect, except that the model with the smallest DIC included the interaction between arrival patch and year rather than their additive effects (Supplementary Material, Tables S1 and S3). Therefore, we only detail here results for models with patch and year of departure.

In this species as in many others, dispersal propensity was strongly sex- and age-biased, with females and yearlings dispersing more / farther than males and older birds respectively (Doligez et al. 1999; Greenwood and Harvey 1982; Part and Gustafsson 1989; Part 1990)(Greenwood & Harvey 1982; Pärt & Gustafsson 1989; Pärt 1990; Doligez et al. 1999). Sex and, for global dispersal, age (as a continuous variable) were therefore included as fixed effects in the models. In a second step, we tried to model the spatio-temporal variance (i.e. variance associated with patch and year effects) in dispersal propensity using two measures of local habitat quality included in the models as fixed effects: (i) local breeding density (i.e. number of breeding pairs in the patch and year considered, because nest boxes were distributed with similar densities in all patches) and (ii) local reproductive success of conspecifics (i.e. mean fledgling number per nest in the patch and year considered). In this population, local breeding density and reproductive success have previously been shown to

relate negatively with departure decisions (Doligez et al. 1999, 2002) and positively with settlement decisions (Doligez et al. 2004).

Animal models were implemented in R software using MCMCglmm package (Hadfield 2010). Because the response variable was binary, we used a binomial model (probit link function). Binary data have been shown not to provide enough information to infer the variance of the liability trait underlying the threshold model. Therefore, we fixed the residual variance to one and consequently, estimated relative variance values rather than absolute values for the additive genetic, patch, year, maternal and individual effects (de Villemereuil et al. 2013). For our binary variable, we used a $\mathcal{V}^2$ distribution with one degree of freedom as the prior distribution, following de Villemereuil et al. (2013), because the frequently used inverse-Gamma prior has the asset of giving too much weight to the value 1 (de Villemereuil et al. 2013). Conversely, the $\mathcal{V}^2$ prior used here had a more balanced distribution. Even though the distribution remains biased (towards 1), the influence of the prior should fade rapidly because of the large data here. We also checked the potential influence of the prior distribution by running the models with patch and year of departure with an inverse-Gamma prior (0.001; 0.001) and we found no difference in heritability estimates between both priors (results not detailed).

Each of the 40 models was run over 5,000,000 iterations with a burn-in of 10,000 and a thinning interval of 100 iterations, thus giving us 49,900 iterations for the estimation of parameters and a final effective sample between 6,000 and 49,000 depending on the factors included in the model. Selection model was based on DIC values provided by MCMCglmm package. We calculated the narrow-sense heritability (h^2) of dispersal propensity as the ratio of the additive genetic variance (V_A) over the sum of estimated variances (V_A, V_{Patch}, V_{Year}, $V_{Patch\ x\ Year}$, V_{Mat} and/or V_I when applicable, depending on models) to which we added the residual variation (V_R, fixed to 1) and the probit link variance (V_{Probit}, equal to 1). The probit link variance was needed to get heritability estimates on the liability scale (Nakagawa and Schielzeth 2010). For instance, for the simplest model including only the additive genetic effect as a random effect, heritability was calculated as follows:

$$h^2 = \frac{V_A}{V_A + V_R + V_{Probit}} = \frac{V_A}{V_A + 1 + 1}$$

Heritability estimates from other models were calculated by adding to the denominator the different sources of variance estimated for random effects included besides the additive

genetic variance. In the results section estimates are given followed by 95% credibility intervals.

Results

Dispersal heritability estimates when including different sources of variance

The simplest model for natal dispersal (with additive genetic variance as the only random effect) and for global dispersal (with additive genetic and individual variances) showed the presence of additive genetic variance (estimate with 95% CI: natal dispersal: 1.20 (0.63; 1.83); global dispersal: 0.60 (0.36; 0.84); first line on Figure 1a and c), corresponding a heritability estimate for natal dispersal propensity of 0.37 (0.25; 0.49) and for global dispersal propensity of 0.22 (0.14; 0.29) (Table 2).

When the effects of maternal identity and/or year of departure were included in the models (lines 3,4 and 8 of each panel on Figure 1), these effects were always associated with small variances (Table 2) and thus had little impact on the dispersal heritability estimate (Figure 1). For natal dispersal, dispersal heritability estimate when adding maternal identity decreased to 0.33 (0.20; 0.46), when adding year to 0.34 (0.23; 0.46) and when adding both maternal identity and year to 0.30 (0.17; 0.43). For global dispersal, dispersal heritability estimate when adding maternal identity decreased to 0.20 (0.12; 0.28), when adding year to 0.21 (0.13; 0.28) and when adding both maternal identity and year to 0.19 (0.11; 0.27).

Conversely, when the effect of patch of departure was included in the model, either alone (line 2 of each panel on Figure 1) or in combination with other random effects (lines 5, 6, 7, 9 and 10 of each panel on Figure 1), it was associated with large variance (natal dispersal: between 24.8 % and 26.1 % ; global dispersal : between 19.2 % and 20.0%; Table 2) and strongly impacted additive genetic variance estimate, thus dispersal heritability estimate (Figure 1). For natal dispersal, dispersal heritability estimate when adding patch decreased to 0.10 (0.00; 0.19), when adding patch, year and maternal identity to 0.08 (0.00; 0.16) and when adding the interaction between patch and year to 0.15 (0.04; 0.26); other combinations yielded similar changes (Table 2a; Figure 1a). For global dispersal, dispersal heritability estimate when adding patch decreased to 0.06 (0.00; 0.12), when adding patch, year and maternal identity to 0.06 (0.00; 0.11) and when adding the interaction between patch and year to 0.09 (0.02-0.17); other combinations yielded similar changes (Table 2b; Figure 1c). The variance associated with the individual identity was however not affected (Figure 1c). The best models as indicated by DIC values were models including the effects of patch, year and maternal identity effects (although the model without maternal identity was also

retained for global dispersal; Table 2); however, model selection should be considered with caution because the computation of DIC implemented in MCMCglmm favours models with high number of random effects.

In all models, sex and, for global dispersal, age (in the departure year) were highly significant (all $P < 0.001$). As expected, males and older individuals were less likely to disperse than females and younger individuals, respectively (Table 3a).

Modelling spatio-temporal environmental variance with local breeding density and success

When we included local breeding density and reproductive success as measures of habitat quality in the models, both effects were significant (all $P < 0.034$; Table 3b). As expected, dispersal propensity decreased when local breeding density and reproductive success increased (Table 3b). Sex and age effects remained significant (Table 3b).

However, the variances associated with patch and year effects were unchanged (Table 4; Figure 1b and d). Other random effects were globally unchanged as well (Table 4). Overall, dispersal heritability estimates slightly decreased compared to models without the effects of local breeding density and reproductive success. For natal dispersal, dispersal heritability estimate when including only additive genetic variance was 0.30 (0.18; 0.43), against 0.37 without local breeding density and reproductive success (Table 4a). For global dispersal, dispersal heritability estimate when including only additive genetic variance was 0.18 (0.10; 0.25), against 0.22 without local breeding density and reproductive success (Table 4b). When the models included patch (resp. year), dispersal heritability estimates were 0.11 (0.00; 0.20) (resp. 0.29 (0.18; 0.41)) for natal dispersal (Table 4a) and 0.07 (0.00; 0.12) (resp. 0.17 (0.10; 0.25)) for global dispersal (Table 4b). For models with other random effects or combinations of random effects, heritability estimates were only slightly affected by the presence of local breeding density and reproductive success in the models (Table 4, Figure 1). The same models were selected than without the effects of local habitat quality measures (i.e. models with patch, year and maternal identity variances on top of additive genetic variance) on the basis of DIC, but the DIC values decreased when including them (Table 4).

Discussion

The level of heritability of a trait conditions its evolutionary potential and it thus an important parameter when addressing its evolution in the wild. Previous studies have shown that heritability is a condition-dependent parameter, rather than a fixed value, including studies on dispersal (e.g. Bitume et al. 2011; Bonte et al. 2007). Here, we investigated to what extent heritability estimates of between-patch dispersal propensity in the collared flycatcher was affected by accounting for different sources of variance, i.e. including different random effects, in the quantitative genetics models ('animal models') estimating heritability. In particular, we expected that including patch and year effects in the models would reduce residual variance. Our results show that year and maternal identity effects had little impact on heritability estimates. Conversely, the variance associated with patch effect, i.e. spatial environmental variation, was large and strongly decreased heritability estimates. Furthermore, including measures of local habitat quality known to affect dispersal propensity in this population (breeding density and reproductive success in the patch) as fixed effects did not reduce the variance associated with patch effect, i.e. did not explain the spatial environmental variation in dispersal propensity. These results suggest that genetic relatedness shows a spatial (patch) structure in this population, explaining why a large part of the additive genetic variance is captured by the variance associated with the patch effect.

Factors affecting dispersal propensity and heritability in the absence of spatio-temporal environmental variance

Our results confirm that the decision to disperse in this population is multi-causal, with external (i.e. environmental) and internal (i.e. individual) factors affecting between-patch dispersal propensity. As in many other bird species, females were more likely to disperse than males (i.e. sex-biased dispersal) and young birds were more likely to disperse than adults (i.e. higher natal dispersal compared to breeding dispersal; Greenwood and Harvey 1982; Paradis et al. 1998) Moreover, as already been found in this population, local habitat quality also triggered dispersal decisions, with lower probability to leave a patch when local density and/or reproductive success was high (Doligez et al. 1999, 2002, 2004). Besides these well-known effects, in the absence of random effects reflecting environmental sources of variation, dispersal propensity in our population showed positive heritability both when natal dispersal was investigated alone and when all dispersal events where considered (i.e. when mixing natal and breeding dispersal). This confirmed previous results on the same population obtained

from parent-offspring regressions (Doligez et al. 2009) or animal models using a frequentist approach (Doligez et al. 2012), even though a Bayesian approach should lead to more reliable results in the case of a binary variable such as here (de Villemereuil et al. 2013). The lower heritability level observed when natal and breeding dispersal are considered together compared to natal dispersal alone can be explained by the influence of personal experience, in particular individual reproductive success, in adults compared to young individuals (Doligez et al. 1999, 2009; Switzer 1997).

Our results are in line with previous studies investigating the genetic basis of dispersal in vertebrates, and more specifically in birds, showing heritability for dispersal (reviews in Doligez and Pärt 2008; Doligez et al. 2012). Dispersal heritability level was usually moderate, varying between 0.15 and 0.60 for studies using an animal model approach (Charmantier et al. 2011; Duckworth and Kruuk 2009; Korsten et al. 2013; McCleery et al. 2004). Estimates obtained from parent-offspring regressions were usually less precise and covered a larger range of values (between 0.05 and 0.88: Doligez et al. 2009; Forero et al. 1999; Greenwood et al. 1979; Hansson et al. 2003; Matthysen et al. 2005; Newton and Marquiss 1983; Pasinelli et al. 2004; Potti and Montalvo 1991; Wheelwright and Mauck 1998). The heritability level obtained here when environmental sources of variance were not modelled fell within this range. Overall, these results emphasize that dispersal is partly genetically determined and thus may evolve under selective pressures differentially affecting the success of dispersing and non-dispersing individuals in various taxa (e.g. Cheptou et al. 2008; Duckworth and Badyaev 2007; Thomas et al. 2001). Such pressures may select for dispersal strategies with dispersal associated with different phenotypic traits, i.e. dispersal syndromes (Clobert et al. 2009), which maintain variation in dispersal within populations. The low to moderate values for dispersal heritability may result from the multi-causal nature of dispersal in relation to the spatio-temporal environmental variation in factors triggering dispersal decisions of individuals with different genetic background (Clobert et al. 2001).

Spatial environmental variance captures additive genetic variance: a spatial structure of relatedness in the study population

When the natal or previous breeding patch was included as a random factor to account for the effect of spatial environmental variation on dispersal propensity, we found that dispersal heritability estimates strongly decreased, both for natal dispersal alone (from 0.37 down to 0.11) and when all dispersal events were considered (from 0.22 down to 0.06). In both cases, the confidence intervals for heritability estimates included 0, meaning that the

genetic basis of dispersal was not firmly supported anymore. Other sources of variation (year, maternal identity) also affected heritability estimates and model selection suggested an effect of all sources of variation, because all were retained in the final model. Nevertheless, the decrease in heritability estimates was highest when the patch effect was included in the models. We expected that spatio-temporal environmental effects would capture part of the unexplained residual variance in dispersal propensity, because dispersal decisions are affected by environmental factors in many species (reviews in Bowler and Benton 2005; Clobert et al. 2001; Ronce 2007), including our study population (e.g. Doncaster et al. 1997). Intriguingly, the relative part of the total variance in dispersal propensity that remained unexplained was unchanged when including environmental sources of variation (patch, year). Rather than capturing residual variance, the patch effect captured a large part of the genetic additive variance (see lines 1 vs. 2 on each panel of Figure 1). The year effect behaved similarly to the patch effect but with a far lower influence (see lines 1 vs. 3 on each panel of Figure 1). In addition, the maternal identity effect also captured part of the additive genetic variance as could be expected, but this effect was far more limited than the patch effect (see lines 1 vs. 4 on each panel of Figure 1).

The observed patterns for patch variance suggest that additive genetic and patch (spatial) variance are partly confounded in our population. Such a pattern should result from non-random relatedness between individuals in space, such that both sources of variance explain the same part of total phenotypic variance in dispersal propensity for the animal model. In other words, individuals within a given patch should show higher relatedness level than individuals over the whole population. This hypothesis of a spatial structure in relatedness between individuals in our study population was confirmed by a Mantel test on natal dispersal events, investigating the distance between the relatedness matrix (obtained from the pedigree), and the matrix describing the similarity in birth patch, i.e. the spatial similarity between individuals (this matrix was filled with 1 if the two individuals considered were born in the same patch and 0 otherwise). Running the Mantel test over 10,000 iterations (ZT software; Bonnet and van de Peer 2002), we obtained a significant correlation despite a small effect size ($r = 0.060$, $P < 0.001$). Thus, related individuals indeed shared the same birth area more than expected at random. However, whether the low observed correlation reflects a sufficient spatial structure in relatedness to explain our result that additive genetic and patch variance are strongly confounded remains uncertain and understanding this result requires additional work to characterize the origin of this spatial structure in relatedness.

Such a spatial structure in relatedness between individuals may result from two different processes: (i) limited dispersal movements in space and/or (ii) similar choice of breeding patch by related individuals. Given that over a third of breeding individuals each year are immigrants into the population (i.e. previously unringed), relatively long-distance dispersal is likely to be frequent, even though part of these unringed individuals are local birds previously missed (see Doligez et al. 2012). In the population, over 60% of yearlings are natal dispersers (i.e. were born in another patch), with frequent high dispersal distances (i.e. over 2 km; Part 1990). Thus a strong spatial structure in relatedness due to limited movements seems unlikely in this population. On the other hand, similar choice of breeding patch by related individual could occur if habitat selection rules are genetically determined, i.e. if the cues used by individuals in dispersal decision-making are heritable. In this case, related individuals would tend to settle in the same patches as a result of using the same cues. In this population as well as in the sister species, the pied flycatcher, the use of information for breeding site selection has been extensively studied (Forsman et al. 2008, 2014; Jaakkonen et al. 2013; Kivelä et al. 2014; Loukola et al. 2012; Seppänen et al. 2011). These studies have in particular emphasized high variation between individuals in information use. The question whether between-individual variation in habitat selection rules is genetically determined remains open and calls for future work aiming at estimating the heritability of information use in breeding habitat selection in this system. Here, maternal identity had a limited influence in shaping variation in dispersal propensity, but this does not preclude a modulation of between-individual variation in habitat selection rules via maternal effects, since such effects may vary within mothers in relation to environmental variation (Mousseau and Fox 1998; e.g. Meylan et al. 2002; Tschirren et al. 2007 for modulation of natal dispersal via maternal hormones), which is difficult to address using animal models.

Recent studies have shown that dispersers are unlikely to be a random sample of a population with respect to different phenotypic (physiological, morphological, behavioural or life-history) traits (Clobert et al. 2009; Edelaar and Bolnick 2012). These traits may in particular help individuals to alleviate the costs of dispersal, leading to the selection of combinations of traits and their integration at the population (i.e. genetic) level (e.g. for personality traits: Duckworth and Kruuk 2009; Korsten et al. 2013; this thesis). Studies frequently report additive genetic variance in dispersal propensity or distance, but which components of the dispersal process exactly are genetically determined remains unknown. Our results suggest that habitat selection rules, i.e. the use of information in making decisions where to settle, may be one important component of such a genetic determinism in our study

system. This is in line with previous results showing that information use may depend on personality traits (e.g. Kurvers et al. 2010), themselves frequently genetically determined (e.g. Bize et al. 2012; Duckworth and Kruuk 2009; Korsten et al. 2010, 2013). Exploring a genetic determinism of habitat selection rules therefore appears as the next step towards understanding the genetic basis for dispersal behaviour.

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Table 1. Statistics for the pedigree of the study population of collared flycatchers on Gotland. These statistics have been computed including only the individuals that are informative to our analyses of the heritability of dispersal propensity (i.e. individuals with known dispersal status selected following the criteria detailed in text). N: number of individuals / observed links. Pedigree maximum depth is the maximum number of generations that separate two related individuals.

Pedigree statistics	**Count**
N individuals	5,572
N maternal links	3,071
N paternal links	3,246
N full sibs	1,014
N maternal sibs	2,089
N maternal half sibs	1,075
N paternal sibs	2,091
N paternal half sibs	1,077
N maternal grandmothers	1,198
N maternal grandfathers	1,239
N paternal grandmothers	1,194
N paternal grandfathers	1,236
Pedigree maximum depth (N generations)	13

Table 2. Variance components for dispersal propensity in the study population of collared flycatchers. Models including only (a) sex as a fixed effect for natal dispersal and (b) sex and age as fixed effects for global dispersal, together with the random effects whose associated variances are shown in each line. Estimates are given with their 95% CI (in parentheses). V_A: additive genetic variance; V_I: individual variance (only for breeding dispersal); V_{Patch}: departure patch variance; V_{Year}: year variance; $V_{Patch\ x\ Year}$: variance associated with the interaction between departure patch and year; V_{Mat}: maternal identity variance. In bold: model(s) with the smallest DIC value.

Model	V_A	V_I	V_{Patch}	V_{Year}	$V_{Patch\ x\ Year}$	V_{Mat}	h^2	DIC
(a) Natal dispersal								
1	1.20 (0.63; 1.83)						0.37 (0.25; 0.49)	3,407
2	0.32 (0.00; 0.63)		0.82 (0.23; 1.64)				0.10 (0.00; 0.19)	3,360
3	0.46 (0.09; 0.90)				0.51 (0.32; 0.72)		0.15 (0.04; 0.26)	3,370
4	0.36(0.00; 0.75)				0.53 (0.33; 0.74)	0.16 (0.00; 0.38)	0.12 (0.00; 0.22)	3,356
5	0.27 (0.00; 0.58)		0.84 (0.24; 1.68)			0.11 (0.00; 0.29)	0.08 (0.00; 0.17)	3,349
6	0.32 (0.00; 0.62)		0.79 (0.23; 1.59)	0.06 (0.00; 0.13)			0.10 (0.00; 0.18)	3,342
7	**0.26 (0.00; 0.58)**		**0.81 (0.22; 1.63)**	**0.06 (0.00; 0.13)**		**0.11 (0.00; 0.29)**	**0.08 (0.00; 0.16)**	**3,332**
8	1.12 (0.51; 1.77)					0.23 (0.00; 0.51)	0.33 (0.20; 0.46)	3,378
9	1.14 (0.57; 1.75)			0.14 (0.04; 0.28)			0.34 (0.23; 0.46)	3,377
10	1.04 (0.44; 1.68)			0.15 (0.04; 0.29)		0.23 (0.00; 0.51)	0.30 (0.17; 0.43)	3,350
(b) Global dispersal								
1	0.60 (0.36; 0.84)	0.14 (0.00; 0.36)					0.22 (0.14; 0.29)	5,370
2	0.19 (0.00; 0.35)	0.21 (0.00; 0.42)	0.60 (0.18; 1.20)				0.06 (0.00; 0.12)	5,227
3	0.28 (0.05; 0.50)	0.25 (0.00; 0.48)			0.39 (0.26; 0.53)		0.09 (0.02; 0.17)	5,213
4	0.24 (0.00; 0.44)	0.23 (0.00; 0.47)			0.39 (0.26; 0.53)	0.06 (0.00; 0.18)	0.08 (0.00; 0.15)	5,211
5	0.17 (0.00; 0.33)	0.20 (0.00; 0.41)	0.60 (0.18; 1.20)			0.04 (0.00; 0.13)	0.06 (0.00; 0.11)	5,226
6	**0.19 (0.00; 0.36)**	**0.22 (0.00; 0.44)**	**0.59 (0.17; 1.20)**	**0.04 (0.00; 0.08)**			**0.06 (0.00; 0.12)**	**5,204**
7	**0.17 (0.00; 0.34)**	**0.20 (0.00; 0.42)**	**0.59 (0.16; 1.17)**	**0.04 (0.00; 0.08)**		**0.04 (0.00; 0.14)**	**0.06 (0.00; 0.11)**	**5,204**
8	0.56 (0.32; 0.81)	0.12 (0.00; 0.34)				0.06 (0.00; 0.18)	0.20 (0.12; 0.28)	5,368
9	0.59 (0.36; 0.84)	0.16 (0.00; 0.38)		0.08 (0.02; 0.16)			0.21 (0.13; 0.28)	5,327

10	0.55 (0.30; 0.80)	0.14 (0.00; 0.36)	0.08 (0.02; 0.16)	0.07 (0.00; 0.20)	0.19 (0.11; 0.27)	5,325

Table 3. Effects of fixed factors on natal and global dispersal propensity in the study population of collared flycatchers: (a) sex and, for global dispersal, age and (b) sex, age and the two measures of habitat quality, local breeding density and reproductive success. *P* values are pMCMC. Results are shown only for the models including as random effects additive genetic variance V_A only (model 1), additive genetic variance V_A and variance associated with departure patch V_{Patch} (model 2) and additive genetic variance V_A together with variances associated with departure patch V_{Patch}, departure year V_{Year} and maternal identity V_{Mat} (model 7; see Tables 2 and 4). Estimates for the sex effect correspond to the value for males compared to females and for the age effect to older adults compared to yearlings. Estimates are given with their 95% CI (in parentheses).

Model	Sex	*P* (sex)	Age	*P* (age)	Density	*P* (density)	Success	*P* (success)	DIC
(a) Without measures of local habitat quality									
Natal dispersal									
1	-0.54 (-0.71; -0.37)	< 0.0001							3,407
2	-0.48 (-0.62; -0.33)	< 0.0001							3,360
7	-0.49 (-0.64; -0.33)	< 0.0001							3,332
Global dispersal									
1	-0.79 (-0.92; -0.66)	< 0.0001	-0.83 (-0.89; -0.76)	< 0.0001					5,370
2	-0.76 (-0.89; -0.64)	< 0.0001	-0.82 (-0.89; -0.75)	< 0.0001					5,223
7	-0.77 (-0.90; -0.64)	< 0.0001	-0.83 (-0.90; -0.76)	< 0.0001					5,204
(b) With measures of local habitat quality									
Natal dispersal									
1	-0.52 (-0.68; -0.35)	< 0.0001			-0.02 (-0.02; -0.01)	< 0.0001	-0.23 (-0.33; -0.14)	< 0.0001	3,399
2	-0.48 (-0.63; -0.33)	< 0.0001			-0.01 (-0.02; -0.01)	0.034	-0.16 (-0.26; -0.07)	0.001	3,352
7	-0.49 (-0.64; -0.33)	< 0.0001			-0.01 (-0.02; -0.00)	0.034	-0.14 (-0.26; -0.04)	0.012	3,328
Global dispersal									
1	-0.77 (-0.89; -0.64)	< 0.0001	-0.84 (-0.91; -0.77)	< 0.0001	-0.01 (-0.02; -0.01)	< 0.0001	-0.21 (-0.28; -0.14)	< 0.0001	5,328
2	-0.76 (-0.88; -0.63)	< 0.0001	-0.83 (-0.90; -0.77)	< 0.0001	-0.01 (-0.02; -0.00)	0.001	-0.16 (-0.23; -0.09)	< 0.0001	5,213
7	-0.77 (-0.90; -0.64)	< 0.0001	-0.84 (-0.91; -0.77)	< 0.0001	-0.01 (-0.02; -0.00)	0.002	-0.15 (-0.23; -0.07)	0.0003	5,199

Table 4. Variance components for dispersal propensity in the study population of collared flycatchers. Models including the two measures of habitat quality (local breeding density and reproductive success) as well as (a) sex as a fixed effect for natal dispersal and (b) sex and age as fixed effects for global dispersal, together with the random effects whose associated variances are shown in each line. Estimates are given with their 95% CI (in parentheses). See table 2 for description of variance components. In bold: model(s) with the smallest DIC value.

Model	V_A	V_I	V_{Patch}	V_{Year}	$V_{Patch\ x\ Year}$	V_{Mat}	h^2	DIC
(a) Natal dispersal								
1	0.90 (0.42; 1.44)						0.30 (0.18; 0.43)	3,399
2	0.33 (0.00; 0.64)		0.64 (0.18; 1.32)				0.11 (0.00; 0.20)	3,352
3	0.41 (0.00; 0.77)				0.38 (0.22; 0.55)		0.14 (0.03; 0.26)	3,365
4	0.31 (0.00; 0.69)				0.39 (0.23; 0.58)	0.18 (0.00; 0.40)	0.10 (0.00; 0.21)	3,346
5	0.26 (0.00; 0.58)		0.66 (0.17; 1.35)			0.12 (0.00; 0.31)	0.08 (0.00; 0.17)	3,340
6	0.33 (0.00; 0.65)		0.63 (0.16; 1.29)	0.05 (0.00; 0.11)			0.11 (0.00; 0.20)	3,340
7	**0.26 (0.00; 0.58)**		**0.64 (0.17; 1.32)**	**0.05 (0.00; 0.11)**		**0.12 (0.00; 0.31)**	**0.08 (0.00; 0.17)**	**3,328**
8	0.81 (0.30; 1.35)					0.21 (0.00; 0.47)	0.26 (0.13; 0.40)	3,375
9	0.89 (0.42; 1.42)			0.08 (0.01; 0.17)			0.29 (0.18; 0.41)	3,378
10	0.79 (0.31; 1.36)			0.09 (0.01; 0.18)		0.21 (0.00; 0.47)	0.25 (0.12; 0.38)	3,355
(b) Global dispersal								
1	0.47 (0.26; 0.69)	0.14 (0.00; 0.36)					0.18 (0.10; 0.25)	5,328
2	0.18 (0.00; 0.34)	0.21 (0.00; 0.42)	0.43 (0.11; 0.86)				0.07 (0.00; 0.12)	5,213
3	0.25 (0.03; 0.046)	0.24 (0.00; 0.48)			0.27 (0.17; 0.39)		0.09 (0.01; 0.16)	5,209
4	0.21 (0.00; 0.40)	0.22 (0.00; 0.46)			0.28 (0.17; 0.39)	0.06 (0.00; 0.17)	0.08 (0.00; 0.14)	5,208
5	0.16 (0.00; 0.33)	0.19 (0.00; 0.41)	0.43 (0.11; 0.87)			0.04 (0.00; 0.13)	0.06 (0.00; 0.11)	5,212
6	**0.19 (0.00; 0.35)**	**0.21 (0.00; 0.43)**	**0.42 (0.11; 0.87)**	**0.03 (0.00; 0.06)**			**0.07 (0.00; 0.12)**	**5,199**
7	**0.16 (0.00; 0.33)**	**0.20 (0.00; 0.41)**	**0.42 (0.11; 0.86)**	**0.03 (0.00; 0.06)**		**0.04 (0.00; 0.13)**	**0.06 (0.00; 0.11)**	**5,199**
8	0.43 (0.22; 0.66)	0.13 (0.00; 0.34)				0.05 (0.00; 0.16)	0.17 (0.09; 0.24)	5,326
9	0.47 (0.25; 0.69)	0.16 (0.00; 0.38)		0.04 (0.00; 0.08)			0.17 (0.10; 0.25)	5,307
10	0.43 (0.20; 0.66)	0.14 (0.00; 0.36)		0.04 (0.00; 0.08)		0.06 (0.00; 0.17)	0.16 (0.08; 0.24)	5,305

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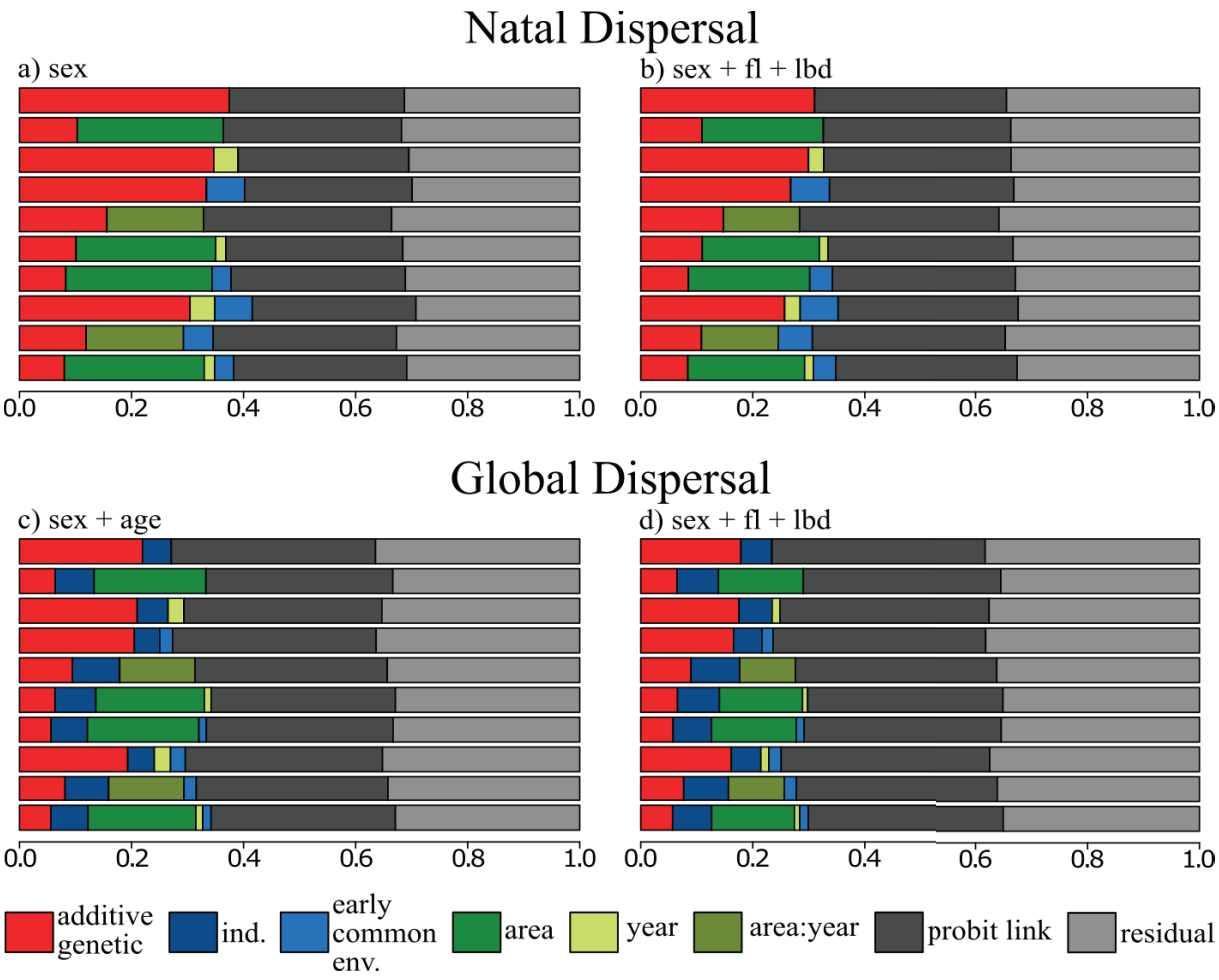
Figure legend

Figure 1. Partitioning of the phenotypic variance of dispersal propensity in the study population of collared flycatchers (after controlling for sex and age when applicable) into the components considered here: additive genetic ($V_{A,}$), departure patch (V_{Patch}), departure year (V_{Year}), maternal identity (V_{Mat}) and individual (V_I) variance (or possibly the combined effect of patch and year $V_{Patch\ x\ Year}$), as well as the residual (V_R) and probit (V_{Probit}) variances. Each line represents one model with the sources of variances illustrated included as random effects (from top to bottom: simplest to most complete model). The figure shows the proportion of the total phenotypic variance for each source of variance (binary data does not allow estimating absolute variance values but only values relative to the residual variance fixed to 1 in the models – see text). Models for natal dispersal (a and b) always included sex, and models for global dispersal (c and d) sex and age, as fixed effects. In addition, local breeding density and reproductive success were added as measures of habitat quality (fixed effects) in models b and d.



Supplementary Material

Figure S1. Partitioning of the phenotypic variance of dispersal propensity in the study population of collared flycatchers (after controlling for sex and age when applicable) into the components considered here: additive genetic ($V_{A,}$), arrival patch (V_{Patch}), arrival year (V_{Year}), maternal identity (V_{Mat}) and individual (V_I) variance (or possibly the combined effect of patch and year $V_{Patch\ x\ Year}$), as well as the residual (V_R) and probit (V_{Probit}) variances. Each line represents one model with the sources of variances illustrated included as random effects (from top to bottom: simplest to most complete model). The figure shows the proportion of the total phenotypic variance for each source of variance (binary data does not allow estimating absolute variance values but only values relative to the residual variance fixed to 1 in the models – see text). Models for natal dispersal (a and b) always included sex, and models for global dispersal (c and d) sex and age, as fixed effects. In addition, local breeding density and reproductive success were added as measures of habitat quality (fixed effects) in models b and d.

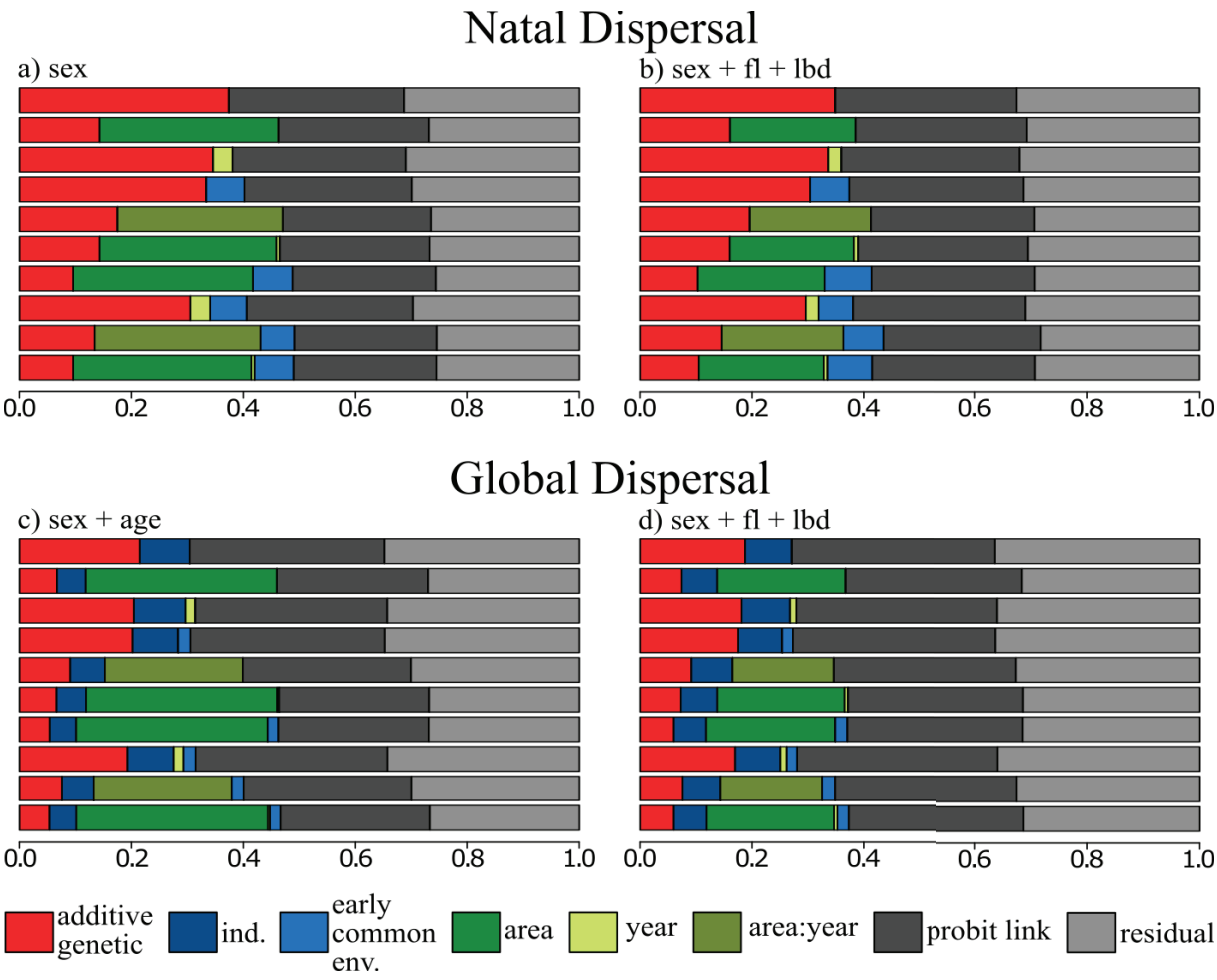


Table S1. Variance components for dispersal propensity in the study population of collared flycatchers. Models including only (a) sex as a fixed effect for natal dispersal and (b) sex and age as fixed effects for global dispersal, together with the random effects whose associated variances are shown in each line. Estimates are given with their 95% CI (in parentheses). V_A: additive genetic variance; V_I: individual variance (only for breeding dispersal); V_{Patch}: arrival patch variance; V_{Year}: arrival year variance; $V_{Patch\ x\ Year}$: variance associated with the interaction between departure patch and year; V_{Mat}: maternal identity variance. In bold: model(s) with the smallest DIC value.

Model	V_A	V_I	V_{Patch}	V_{Year}	$V_{Patch\ x\ Year}$	V_{Mat}	h^2	DIC
(a) Natal dispersal								
1	1.20 (0.62; 1.82)						0.37 (0.25; 0.49)	3,408
2	0.53 (0.14; 0.94)		1.19 (0.36; 2.34)				0.14 (0.05; 0.24)	3,180
3	0.66 (0.20; 1.16)				1.12 (0.75; 1.52)		0.17 (0.07; 0.27)	3,131
4	**0.53 (0.00; 1.00)**				**1.17 (0.78; 1.59)**	**0.24 (0.00; 0.52)**	**0.13 (0.01; 0.24)**	**3,107**
5	0.37 (0.00; 0.76)		1.26 (0.36; 2.45)			0.28 (0.00; 0.54)	0.09 (0.00; 0.19)	3,153
6	0.53 (0.16; 0.97)		1.18 (0.36; 2.33)	0.02 (0.00; 0.07)			0.14 (0.05; 0.24)	3,176
7	0.38 (0.00; 0.78)		1.25 (0.38; 2.47)	0.02 (0.00; 0.07)		0.27 (0.00; 0.53)	0.09 (0.00; 0.19)	3,150
8	1.12 (0.52; 1.78)					0.23 (0.00; 0.51)	0.33 (0.19; 0.46)	3,378
9	1.12 (0.58; 1.74)			0.11 (0.01; 0.23)			0.34 (0.22; 0.46)	3,397
10	1.03 (0.45; 1.67)			0.12 (0.01; 0.25)		0.22 (0.00; 0.50)	0.30 (0.17; 0.43)	3,370
(b) Global dispersal								
1	0.62 (0.36; 0.89)	0.26 (0.00;0.52)					0.21 (0.13; 0.30)	5,619
2	0.25 (0.05; 0.44)	0.19 (0.00; 0.42)	1.27 (0.35; 2.56)				0.07 (0.01; 0.13)	5,367
3	0.30 (0.08; 0.53)	0.21 (0.00; 0.46)			0.82 (0.59; 1.07)		0.09 (0.02; 0.16)	5,281
4	**0.25 (0.00; 0.45)**	**0.19 (0.00; 0.44)**			**0.82 (0.58; 1.07)**	**0.07 (0.00; 0.19)**	**0.08 (0.00; 0.13)**	**5,279**
5	0.20 (0.00; 0.38)	0.18 (0.00; 0.40)	1.27 (0.34; 2.53)			0.07 (0.00; 0.19)	0.06 (0.00; 0.11)	5,364
6	0.25 (0.05; 0.45)	0.20 (0.00; 0.43)	1.27 (0.34; 2.56)	0.01 (0.00; 0.04)			0.07 (0.00; 0.12)	5,362
7	0.20 (0.00; 0.38)	0.18 (0.00; 0.41)	1.28 (0.33; 2.58)	0.01 (0.00; 0.04)		0.07 (0.00; 0.19)	0.05 (0.00; 0.11)	5,359
8	0.58 (0.32; 0.86)	0.24 (0.00; 0.49)				0.06 (0.00; 0.18)	0.20 (0.11; 0.29)	5,618
9	0.59 (0.33; 0.86)	0.27 (0.00; 0.53)		0.05 (0.00; 0.11)			0.20 (0.12; 0.29)	5,604
10	0.56 (0.29; 0.84)	0.24 (0.00; 0.51)		0.05 (0.00; 0.12)		0.06 (0.00; 0.18)	0.19 (0.10; 0.28)	5,604

Table S2. Effects of fixed factors on natal and global dispersal propensity in the study population of collared flycatchers: (a) sex and, for global dispersal, age and (b) sex, age and the two measures of habitat quality, local breeding density and reproductive success. *P* values are pMCMC. Results are shown only for the models including as random effects additive genetic variance V_A only (model 1), additive genetic variance V_A and variance associated with arrival patch V_{Patch} (model 2) and additive genetic variance V_A together with variances associated with the interaction between arrival patch and arrival year $V_{Patch \times Year}$ and maternal identity V_{Mat} (model 4; see Tables S1 and S3). Estimates for the sex effect correspond to the value for males compared to females and for the age effect to older adults compared to yearlings.

Model	Sex	*P* (sex)	Age	*P* (age)	Density	*P* (density)	Success	*P* (success)	DIC
(a) Without measures of local habitat quality									
Natal dispersal									
1	-0.54 (-0.71; -0.37)	< 0.0001							3,408
2	-0.48 (-0.62; -0.33)	< 0.0001							3,180
4	-0.56 (-0.76; -0.38)	< 0.0001							3,107
Global dispersal									
1	-0.68 (-0.82; -0.55)	< 0.0001	-0.64 (-0.70; -0.57)	< 0.0001					5,619
2	-0.64 (-0.77; -0.52)	< 0.0001	-0.62 (-0.68; -0.56)	< 0.0001					5,367
4	-0.69 (-0.82; -0.56)	< 0.0001	-0.65 (-0.72; -0.59)	< 0.0001					5,279
(b) With measures of local habitat quality									
Natal dispersal									
1	-0.51 (-0.68; -0.34)	< 0.0001			-0.03 (-0.03; -0.02)	< 0.0001	-0.17 (-0.26; -0.08)	0.0003	3,273
2	-0.48 (-0.64; -0.32)	< 0.0001			-0.02 (-0.03; -0.02)	< 0.0001	-0.02 (-0.12; 0.06)	0.598	3,157
4	-0.55 (-0.72; -0.37)	< 0.0001			-0.03 (-0.04; -0.02)	< 0.0001	-0.17 (-0.32; -0.02)	0.0267	3,085
Global dispersal									
1	-0.67 (-0.80; -0.53)	< 0.0001	-0.65 (-0.72; -0.59)	< 0.0001	-0.02 (-0.02; -0.02)	< 0.0001	-0.13 (-0.19; -0.06)	< 0.0001	5,498
2	-0.64 (-0.76; -0.52)	< 0.0001	-0.62 (-0.69; -0.56)	< 0.0001	-0.02 (-0.03; -0.01)	< 0.0001	-0.04 (-0.11; 0.03)	0.240	5,340
4	-0.68 (-0.82; -0.56)	< 0.0001	-0.66 (-0.73; -0.59)	< 0.0001	-0.03 (-0.04; -0.02)	< 0.0001	-0.15 (-0.27; -0.04)	0.010	5,25

Table S3. Variance components for dispersal propensity in the study population of collared flycatchers. Models including the two measures of habitat quality (local breeding density and reproductive success) as well as (a) sex as a fixed effect for natal dispersal and (b) sex and age as fixed effects for

global dispersal, together with the random effects whose associated variances are shown in each line. Estimates are given with their 95% CI (in parentheses). See table S1 for description of variance components. In bold: model(s) with the smallest DIC value.

Model	V_A	V_I	V_{Patch}	V_{Year}	$V_{Patch\ x\ Year}$	V_{Mat}	h^2	DIC
(a) Natal dispersal								
1	1.07 (0.52; 1.68)						0.34 (0.22; 0.47)	3,273
2	0.52 (0.14; 0.95)		0.73 (0.20; 1.46)				0.16 (0.05; 0.26)	3,157
3	0.67 (0.20; 1.18)				0.74 (0.47; 1.03)		0.19 (0.08; 0.30)	3,108
4	**0.52 (0.00; 1.00)**				**0.77 (0.48; 1.08)**	**0.25 (0.00; 0.54)**	**0.14 (0.01; 0.25)**	**3,085**
5	0.35 (0.00; 0.74)		0.78 (0.22; 1.57)			0.29 (0.00; 0.55)	0.10 (0.00; 0.20)	3,131
6	0.52 (0.14; 0.95)		0.73 (0.19; 1.46)	0.02 (0.00; 0.07)			0.16 (0.05; 0.26)	3,153
7	0.36 (0.00; 0.75)		0.76 (0.19; 1.46)	0.02 (0.00; 0.07)		0.27 (0.00; 0.53)	0.10 (0.00; 0.20)	3,128
8	0.97 (0.41; 1.63)					0.22 (0.00; 0.50)	0.30 (0.16; 0.43)	3,248
9	1.05 (0.50; 1.67)			0.07 (0.00; 0.15)			0.33 (0.21; 0.45)	3,259
10	0.96 (0.38; 1.59)			0.07 (0.00; 0.16)		0.20 (0.00; 0.47)	0.29 (0.16; 0.43)	3,239
(b) Global dispersal								
1	0.51 (0.27; 0.76)	0.23 (0.00;0.49)					0.18 (0.10; 0.27)	5,498
2	0.23 (0.03; 0.43)	0.20 (0.00; 0.44)	0.72 (0.17; 1.53)				0.07 (0.01; 0.14)	5,340
3	0.28 (0.06; 0.51)	0.22 (0.00; 0.48)			0.55 (0.38; 0.74)		0.09 (0.02; 0.16)	5,260
4	**0.23 (0.00; 0.43)**	**0.21 (0.00; 0.46)**			**0.56 (0.39; 0.75)**	**0.07 (0.00; 0.20)**	**0.08 (0.00; 0.14)**	**5,258**
5	0.19 (0.00; 0.36)	0.18 (0.00; 0.42)	0.73 (0.18; 1.55)			0.07 (0.00; 0.18)	0.06 (0.00; 0.12)	5,338
6	0.23 (0.03; 0.43)	0.21 (0.00; 0.45)	0.72 (0.17; 1.53)	0.02 (0.00; 0.05)			0.07 (0.01; 0.14)	5,332
7	0.19 (0.00; 0.36)	0.19 (0.00; 0.42)	0.73 (0.18; 1.54)	0.02 (0.00; 0.05)		0.07 (0.00; 0.18)	0.06 (0.00; 0.12)	5,330
8	0.48 (0.23; 0.74)	0.22 (0.00; 0.47)				0.05 (0.00; 0.16)	0.17 (0.09; 0.26)	5,497
9	0.50 (0.26; 0.75)	0.24 (0.00; 0.50)		0.03 (0.00; 0.07)			0.18 (0.10; 0.26)	5,486
10	0.47 (0.22; 0.73)	0.23 (0.00; 0.48)		0.03 (0.00; 0.07)		0.05 (0.00; 0.16)	0.17 (0.08; 0.25)	5,485

CHAPITRE 2

Negative phenotypic and genetic correlation between natal dispersal propensity and nest defence behaviour in a wild bird

Grégory DANIEL[1,2], Pierre BIZE[3*], Vincent A. VIBLANC[3] and Blandine DOLIGEZ[1]

In prep.

Negative phenotypic and genetic correlation between natal dispersal propensity and nest defence behaviour in a wild bird

Grégory DANIEL[1,2], Pierre BIZE[3*], Vincent A. VIBLANC[3] and Blandine DOLIGEZ[1]

1 CNRS, Department of Biometry and Evolutionary Biology, UMR 5558, Université de Lyon, Université Lyon 1, 43 boulevard du 11 novembre 1918, Bâtiment Gregor Mendel, 69 622 Villeurbanne cedex, France

2 Animal Ecology, Department of Ecology and Genetics, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18d, 752 36 Uppsala, Sweden

3 Department of Ecology and Evolution, University of Lausanne, Biophore, 1015 Lausanne, Switzerland

* Corresponding author

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Abstract

Natural selection is expected to favour the integration between dispersal and phenotypic traits allowing individuals to reduce the impact of dispersal costs. Accordingly, associations have been found between dispersal and personality traits such as aggressiveness and exploration, which may ease settlement in a new environment. However, the nature of these associations has only rarely been explored. Here, we investigated the link between individual personality in nest-defence behaviour and natal dispersal propensity both at a phenotypic and genetic level in a long lived colonial bird, the Alpine swift (*Apus melba*), to provide insights on the potential genetic constraints shaping the co-evolution of these two traits. We found a negative association between natal dispersal and nest-defence both at the phenotypic and genetic level, which suggests the integration of those two traits in a dispersal behavioural syndrome. A negative association between natal dispersal and nest-defence (i.e. risk taking) behaviour may result from direct selection, if being prudent benefits natal dispersers by reducing the costs of settlement in an unfamiliar environment, or from indirect selection, if individuals with lower levels of nest-defence also show lower levels of e.g. aggressiveness, reducing costs of settlement among unfamiliar neighbours in a colony. In both cases, our results support the idea that dispersing individuals are not a random subset of the population, which can have important consequences on the dynamics of spatially structured populations.

Introduction

Natal dispersal, the movement of individuals from their birth to first breeding site [1], is a fundamental process affecting population dynamics and evolution [2,3], notably through the colonization of novel environments [4]. Because dispersal entails costs [5], recent evidence suggests that natural selection may favour the functional integration of dispersal with other phenotypic traits that allow individuals to reduce these costs [6]. In particular, personality or temperament traits, defined as consistent behavioural differences between individuals over time and across contexts in aggressiveness, exploratory behaviour, boldness, activity and/or sociability [6], may affect the success of dispersing individuals when settling and breeding in novel habitats [6,8–10]. Moreover, the fitness returns of different life-history strategies, in particular associated with dispersal, have also been suggested to favour the evolution of animal personalities [11,12]. Consistently, studies in various taxa have reported associations between dispersal and personality traits [6,13]. The origin of these associations however often remains poorly investigated.

Natal dispersal and personality traits can be associated at the phenotypic level if, for instance, behaving more aggressively towards conspecifics or being more prone to explore the environment enables dispersing individuals to acquire a breeding territory more easily or get familiar with an unknown environment and better exploit it subsequently [6,8]. Because natal dispersal and personality traits are often heritable [10,14–18], the (co)evolution of natal dispersal and personality traits may also be constrained by genetic linkage [10,19–21]. The functional integration of these traits at the individual (phenotypic) level may be partly explained by genetic correlation between them at the population level, as is the case between colonisation ability at a large scale and aggressiveness in western bluebirds (*Sialia mexicana*) [16]. On the other hand, genetic correlations do not always lead to phenotypic correlations, as is the case for natal dispersal distance and exploratory behaviour in great tits (*Parus major*) [10]. Although personality traits are defined by their within-individual consistency, there is nonetheless scope for behavioural deviation (i.e. plasticity) around an average behavioural response [22]. Therefore, the phenotypic expression of a genetic association between dispersal and personality traits may also depend on environmental variation and selective pressures acting on dispersal, as is the case between dispersal and nest defence against a dummy predator in collared flycatchers (*Ficedula albicollis*), where dispersing individuals, but not philopatric ones, increasing nest defence against a dummy predator when food-supplemented ([23]; see also [24]). In a rapidly changing environment, insight on the nature of the

associations between natal dispersal propensity and personality traits is crucial in understanding how dispersal by a non-random sample of genotypes may shape population-level processes, such as the distribution and range expansion of a species [6,10,16,25].

Here, working both at a phenotypic and genetic level, we tested for the covariance of individual personality in nest-defence behaviour and natal dispersal propensity in a long lived colonial bird, the Alpine swift (*Apus melba*), to provide insights on the potential genetic constraints shaping the co-evolution of these two traits.

Materiel and Methods

Study model and study population

The Alpine swift is a migratory apodiform bird breeding in colonies of up to several hundreds of pairs in cliff cavities or under the roof of tall buildings in Southern Europe and South-Western Asia. Since 1999, we have monitored swifts in two Swiss colonies located 21 km apart, in the clock towers of Bienne (*ca.* 100 breeding pairs; 47°10'N, 7°12'E) and Solothurn (*ca.* 50 breeding pairs; 47°12'N, 7°32'E). Alpine swifts become sexually mature at the age of 2 or 3 years [26]. Adult swifts return to their previous colony [27] (no breeding dispersal event was observed out of 2,064 breeding events in the two close-by study colonies since 1999 despite almost perfect individual detection; [27]), where they produce a single clutch of one to four eggs per year [17,27]. Alpine swifts are socially monogamous with males and females sharing equally their investment in parental care from incubation onwards. Alpine swifts build open nests that parents defend against predators such as rats, cats, corvids and stone martens [28]. Nest-defence behaviour is highly variable between individuals in this species but partly genetically determined [17]. Each year, nests in the two study colonies are visited regularly to record breeding data, catch parents (during incubation or brooding young nestlings) for identification and measurements, as well as ring and measure young (when 10 days old). Feathers or blood are sampled to sex individuals from DNA [29]. For more information about the study population monitoring, see [17,27].

Measures of natal dispersal and nest defence behaviour

Natal dispersal status was defined here by a change of colony between birth and first breeding (disperser) or not (non-disperser), i.e. a binary variable. Natal dispersal status was known for 648 individuals ringed as nestlings. Because adult Alpine swifts do not disperse once settled and because all nestlings are ringed in the two study colonies, immigrants, i.e. previously unringed adults, were included as natal dispersers into the analyses (N = 295).

Between 2003 and 2014, the nest defence behaviour of breeders was estimated along a shy-bold axis by a single observer (PB) as a 5-level score based on their reaction to a human approach and hand capture [17,30]. Shy individuals that flushed from the nest immediately upon first detection of the observer were assigned the minimal score (0) and individuals that behaved boldly towards the observer during both approach and capture (i.e. moved towards the observer's hand, flapped their wings and clawed on the approaching hand) were assigned the maximal score (2). Individuals behaving intermediately were assigned a score of 0.5 when they remained on the nest during the observer's approach but flushed before capture, a score of 1 when they remained motionless during approach and thus were captured on nest and a score of 1.5 when they remained motionless during approach but subsequently started to move toward the observer when extending the hand for capture (details in [17]). Although scored as a discrete variable, nest-defence variation was most likely continuous as shown by the large inter- and intra-individual variance in behavioural scores of repeatedly captured individuals [17]. Nest-defence score was estimated in 3096 occasions on 759 individuals with known natal dispersal status over the study period, averaging 4.1 ± 3.3 (SD) observations per individual (if an individual was measured more than once in a year, the mean score was computed per individual per year).

Statistical analyses

At the phenotypic scale, we tested whether nest-defence score differed between natal dispersers and locally born individuals using a linear mixed model. We used the mean score per individual as the dependent variable, because nest-defence behaviour is repeatable in this population [17] (see Supplementary Material). In addition to natal dispersal status, the model included sex as a covariate and breeding colony as a random effect, because both have been shown to affect nest-defence behaviour in this population [17]. We however did not include year and hour of capture [17] because the scores for a given individual were recorded at different hours and in different years.

To estimate the genetic correlation between natal dispersal and nest-defence behaviour, we used a quantitative genetics mixed model, the 'animal model' [23, 24], which allows

partitioning the total phenotypic variance of a trait (V_P) into additive genetic (V_A) and environmental variance components, based on the degree of relatedness between individuals obtained from their pedigree. We used here the social pedigree including 6542 individuals, among which 826 had their nest-defence score measured (see Supplementary Table S1 for statistics on the pedigree). We used a bivariate model with natal dispersal status (binary trait) and mean nest-defence score (continuous trait) as response variables. The model included sex as a fixed effect because it is known to affect both response variables [1,17] and breeding colony (V_{COL}) as a random effect in addition to the additive genetic variance, to account for a permanent environment effect affecting nest-defence behaviour [17].

Effects and variances were estimated with a Bayesian approach using MCMCglmm R package [31], starting with uninformative priors. Because binary data do not provide enough information to infer the variance of the liability trait underlying the threshold model (probit link), we fixed the residual variance for the natal dispersal status to one and thus estimated relative variances for the additive genetic and colony effects [32]. For the residual variance of the continuous nest-defence score (Gaussian link), we used a flat prior (V=diag(2) and nu=0). Finally, we used an inverse-Gamma (0.5, 0.5) and a quasi-Beta (0.5, 0.5) distribution for variance and covariance of additive genetic and colony effects, respectively. To compute the posterior distribution, the model was run over 5×10^7 iterations, with a burn-in of 10,000 and a thinning interval of 300, to obtain an effective sample size between 14,900 and 49,900 with an autocorrelation level between iterations less than 0.1 (except for additive genetic variance of natal dispersal for which it was 0.36). The R package provides the posterior mean for each variable and its 95% Credibility Interval (CI), as well as a *P*-value for fixed effects.

The model was parametrized to estimate variance and covariance of the additive genetic random effect and variance only for the colony effect. The narrow-sense heritability of each trait was calculated as V_{Ai}/V_{Pi}, with $V_{Pi} = V_{Ai} + V_{COLi} + V_{Ri}$, where i is the trait considered. The genetic covariance between natal dispersal status and nest-defence behaviour was calculated as $COV_{A1,2}$ / (sqrt(V_{A1}*V_{A2})), where $COV_{A1,2}$ is the additive genetic covariance between the two response traits, V_{A1} the additive genetic variance of trait 1 and V_{A2} the additive genetic variance of trait 2.

Results

Phenotypic relation between natal dispersal status and nest defence behaviour

We found a significant phenotypic association between natal dispersal status and nest-defence behaviour ($F_{1,755}$ = 16.694 P < 0.001). Locally born individuals exhibit stronger nest-defence (i.e. were bolder) than natal dispersers (mean behavioural score ± SE for locally born and natal dispersers respectively: 0.755 ± 0.020 and 0.587 ± 0.024). As previously reported in the same study population [17], females were bolder than males (estimate ± SE for males compared to females: -0.060 ± 0.031; $F_{1,755}$ = 3.86, P = 0.050) and breeding colony explained a significant part of the total variance in mean nest defence behaviour (L = 24.57, df=1, P < 0.001).

Heritability and genetic correlation between natal dispersal status and nest defence behaviour

Accounting for the sex effect on both nest-defence behaviour and natal dispersal status (Table 1), the bivariate animal model showed positive heritability for both traits, as well as a negative genetic correlation between them. Concerning natal dispersal, the relative additive genetic and colony variances (95% CI) were 3.05 (0.74; 6.60) and 1.57 (0.07; 5.05) respectively (with residual variance fixed to 1, see above; Table 1; Figure 1), corresponding to a conditional heritability value of 0.56 (0.25; 0.84). The contribution of additive genetic variance to the overall phenotypic variance for nest-defence behaviour was low, 0.10 (0.07; 0.13) compared to the common environment (breeding colony) effect, 0.93 (0.06; 2.95) (Table 1; Figure 1). Consequently, the conditional heritability of nest-defence behaviour was low, 0.16 (0.01; 0.32). The genetic correlation between natal dispersal status and nest-defence behaviour was estimated to -0.32 (-0.46; -0.17).

Discussion

Using a 12-year data base on natal dispersal and nest defence behaviour in two natural populations of Alpine swifts, we show that natal dispersers were less prone to defend their nest (i.e. take less risk) against a human intruder when compared to locally-born individuals. This negative association between natal dispersal and nest defence was found at both the phenotypic

and genetic levels, which suggests the integration of those two traits in a dispersal behavioural syndrome [33]. Natal dispersal and nest defence behaviour show, respectively, moderate (h^2 = 0.56) and low (h^2 = 0.16) conditional heritability levels that are in line with mean heritability estimates reported in various taxa for dispersal (e.g. [34–36] ; reviews in [15,18]) and risk taking behaviour related to predator avoidance and nest defence (e.g. [30,37,38]). Altogether, these finding provide strong support to the idea that dispersing individuals are not a random subset of the population, which can have important consequences on the dynamics of spatially structured populations [9,13,25]. Accordingly, our results also show significant differences in the propensity to disperse and to take risk during nest defence between the two Alpine swift colonies under investigation (see also [17]). Information on additional colonies may offer a unique opportunity to test how dispersal syndromes influence the dynamics of a meta-population using the Alpine swifts as an example.

Natal dispersal involves three successive behavioural stages: (i) departure from the natal patch, (ii) movement between patches and (iii) settlement in a novel patch [2,3]. Because each dispersal stage is associated with different costs [5], selection may favour the functional integration of dispersal with different phenotypic traits depending on the stage considered and the type of costs to be reduced [13]. In this study, individuals showed natal dispersal only, therefore nest defence behaviour was expressed after lifetime breeding settlement. Hence, one hypothesis explaining the negative association between natal dispersal and nest defence behaviour is that selection favours the direct negative integration of nest defence behaviour with natal dispersal if being prudent can help natal dispersers to reduce the costs of settlement in an unfamiliar environment. Nest predation is an important source of offspring mortality in birds [39], including swifts [28]. However, during the present study, nest predation was rare in Bienne and virtually null in Solothurn, questioning the importance of nest predation as a major selective force driving the present results. Behavioural syndrome theory points out that variation in nest-defence behaviour may also be tightly linked with one or more other major behavioural axes, such as sociability, aggressiveness or exploration [40,41]. Thus, an alternative hypothesis is that indirect selection is accounting for an association between dispersal and nest-defence behaviour, for instance if individuals with lower levels of nest-defence (i.e. risk taking) also show lower levels of aggressiveness, allowing them to settle more easily in a colony, among unfamiliar neighbours. Evidence for direct selection favouring the integration of dispersal with exploratory behaviour has been reported in the great tit [10] and with aggressiveness in the western bluebird [42]. Much remains to be done in the Alpine swift to describe the association between nest-defence and major behavioural axes, and thus to tease

apart the contribution of direct and indirect selection in linking natal dispersal to nest-defence behaviour.

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Table 1. Estimates of fixed effects, variance components, heritability and genetic correlation for natal dispersal status and nest defence behaviour in the Alpine swift study populations, obtained from the bivariate animal model. The table gives the mean posterior distribution and its 95% credible interval, effective sample of the posterior distribution and, for fixed effects, *P*-value (pMCMC).

Variable	Posterior mean	95% CI	Effective sample size	pMCMC
(a) Natal dispersal				
Fixed				
Intercept	0.032	1.630; 1.726	3300	NS
Sex	0.391	-0.011; 0.782	2164	0.030
Random				
Additive genetic	3.046	0.743; 6.601	1064	
Breeding colony	1.574	0.073; 5.047	3300	
h^2	0.564	0.254; 0.836		
(b) Nest defence behaviour				
Fixed				
Intercept	0.697	-0.615; 2.077	3300	NS
Sex	-0.069	-0.129; 0.013	3300	0.024
Random				
Additive genetic	0.098	0.068; 0.131	3300	
Breeding colony	0.933	0.056; 0.120	3300	
h^2	0.160	0.007; 0.320		
(c) Genetic correlation	**-0.322**	**-0.463; -0.166**		

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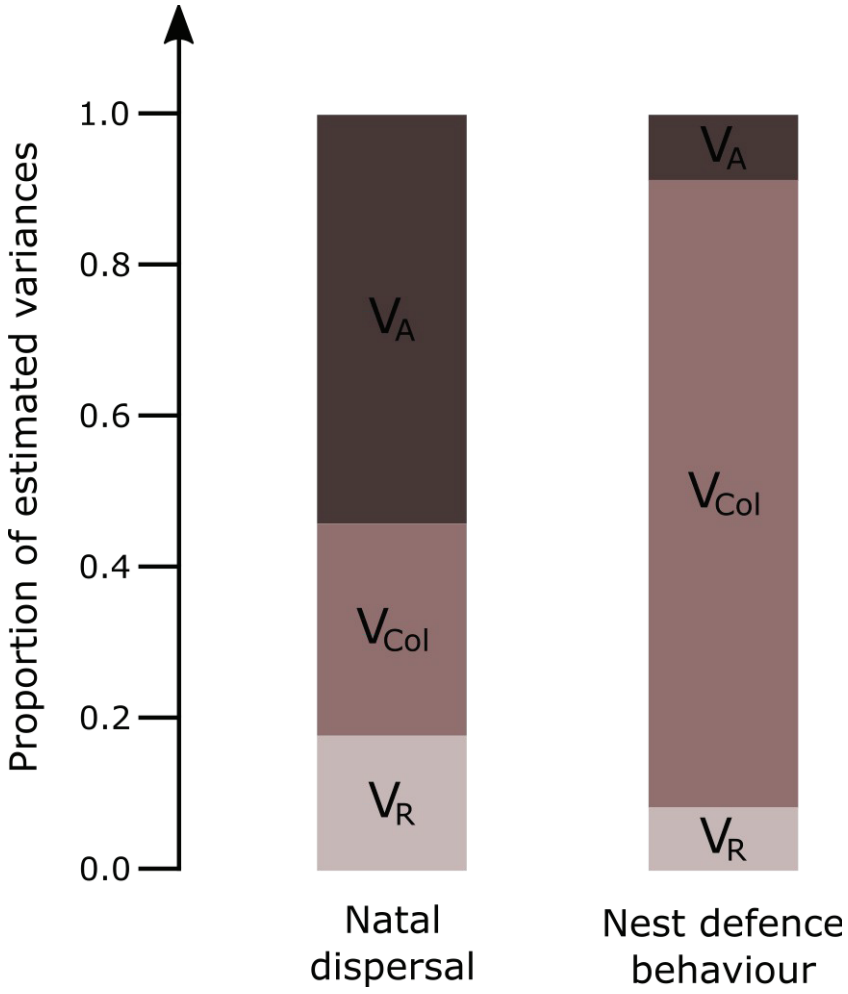
Figure Legend

Figure 1. Relative estimated sources of variances in natal dispersal status and nest defence behaviour in the Alpine Swift study populations. This graph represents the relative part in the total phenotypic variance (V_P, corresponding to 1, or 100%, here) of each source of variance included in the model for the two traits of interest. V_A: additive genetic variance, V_{COL}: variance linked to breeding colony, V_R: residual variance. Proportions of the total phenotypic variance are represented here to allow comparison between the two traits and because only relative values of variances can be obtained for our binary variable (natal dispersal status; see text).



Supplementary material

Repeatability of nest-defence behaviour

The repeatability of nest-defence behaviour was estimated using a linear mixed model (LMM), with nest-defence score as the dependent variable and individual identity as a random factor. Sex, breeding colony, capture hour and capture hour^2 were included as fixed effects because they had previously been found to influence nest defence behaviour [1]. This model estimated the variance due to individuals (between-individual variance; V_I) and the residual variance (within-individual variance; V_R). Repeatability was calculated as V_I / V_P [2], where V_P is the total phenotypic variance of the trait, here $V_I + V_R$. We used the MCMCglmm R package [3] to run this analysis, starting with uninformative priors (see text). To compute the posterior distribution, the model was run over 10^6 iterations, with a burn-in of 100,000 and a thinning interval of 100, to obtain an effective sample size of 9,000 with an autocorrelation level between iterations less than 0.1

We obtained an estimate of 0.103 (95% CI: 0.087-0.120) for V_I and 0.155 (0.146-0.163) for V_R. Nest-defence score was thus repeatable (r = 0.399, 95% CI: 0.355-0.440). This result confirmed over a larger number of years the repeatability previously estimated [1] and supported the use of the mean nest-defence score as the response variable in the animal model for estimating genetic covariance with natal dispersal status. The value obtained for repeatability here was higher than in [1] over 2003-2010, i.e. 0.275. This difference may be due to the lower sample in the Bize et al study [1] and/or the estimation method used (ASReml in [1] vs. Bayesian inference here; see [4]).

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Table S1: Statistics for the pedigree of the Apine swift study populations. This table summarizes the statistics (N: number of individuals / links) for the pedigree including only individuals that are informative with respect to our estimation of the genetic covariance between natal dispersal status and nest defence behaviour. Maximum depth is the maximum number of generations that separate two related individuals. These statistics were computed in R with pedantics package [5].

Pedigree statistics	**Count**
N individuals	826
N maternal links	321
N paternal links	318
N full sibs	118
N maternal sibs	226
N maternal half sibs	108
N paternal sibs	222
N paternal half sibs	104
N maternal grandmothers	93
N maternal grandfathers	92
N paternal grandmothers	56
N paternal grandfathers	56
Maximum depth (N generations)	4

CHAPITRE 3

Do colonizing individuals show specific behavioural profiles? A small-scale experiment testing for dispersal behavioural syndromes in a natural bird population

Grégory DANIEL[1,2], Marion GERMAIN[1,2], Lars GUSTAFSSON[2] and Blandine DOLIGEZ[1,*]

In prep.

Do colonizing individuals show specific behavioural profiles? A small-scale experiment testing for dispersal behavioural syndromes in a natural bird population

Grégory DANIEL[1,2], Marion GERMAIN[1,2], Lars GUSTAFSSON[2] and Blandine DOLIGEZ[1,*]

[1] CNRS, Department of Biometry and Evolutionary Biology, UMR 5558, Université de Lyon, Université Lyon 1, 43 boulevard du 11 novembre 1918, Bâtiment Gregor Mendel, 69622 Villeurbanne cedex, France

[2] Animal Ecology, Department of Ecology and Genetics, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18d, 75236 Uppsala, Sweden

* Corresponding author

Key-words

Personality traits, aggressiveness, neophobia, phenotypic integration, immigration, colonization, behavioural scoring, collared flycatcher, *Ficedula albicollis*

Running head

Behavioural profiles of dispersers

Introduction

Dispersal, defined as the movement of individuals from their birth site (natal dispersal) or their previous breeding site (breeding dispersal) to a new breeding site (Greenwood and Harvey 1982), has long been recognized as a major trait affecting individual and gene flow between populations, thus population dynamics and genetic structure (Bowler and Benton 2005; Clobert et al. 2001; Edelaar and Bolnick 2012; Ronce 2007). In particular, dispersal is a powerful way to cope with environmental variation at various spatial scales, allowing individuals to escape degrading local conditions and colonize new habitats, thereby shaping the dynamics of species spatial distribution (Clobert et al. 2012; Duckworth and Badyaev 2007; Kokko and López-Sepulcre 2006). Selective pressures acting on dispersal evolution can therefore either constrain or accelerate the response to environmental changes in terms of species range dynamics (Kokko and López-Sepulcre 2006). Each stage of the dispersal process (departure, movement, settlement) can entail costs linked to (i) the development of structures allowing increased mobility for departure (e.g. wings), (ii) increased energy expenditure or mortality risk during movement (e.g. higher predation or collision risks) and/or (iii) non-optimal decision-making due to lack of familiarity with, or local maladaptation in, the settlement site (Bonte et al. 2012). Selection is therefore expected to favour the functional integration between dispersal and phenotypic (morphological, physiological, behavioural and/or life-history) traits allowing individuals to reduce these costs and disperse successfully to new habitat patches / sites (Clobert et al. 2009; Duckworth and Badyaev 2007).

Among these traits, behavioural traits such as aggressiveness, exploration behaviour, risk-taking and sociability have recently received increased interest because they were suggested to help dispersers cope with settlement costs (Cote et al. 2010). Increased aggressiveness can increase the chances to secure a breeding site in response to con-and/or heterospecific competition (Duckworth and Badyaev 2007). Increased exploration behaviour can help individuals to get familiar with their new environment more rapidly (Dingemanse et al. 2003). Reduced risk-taking may allow individuals to allocate higher energy and resources in offspring provisioning, especially under constrained conditions (Récapet et al. In prep; this thesis). Finally, sociability may allow individuals to tolerate unfamiliar individuals, especially when densities are high (Cote et al. 2010). All these traits may be correlated to each other (e.g. Garamszegi et al. 2016 in press; Verbeek et al. 1996), characterizing behavioural syndromes that may strongly affect the response of individuals to environmental changes (Sih et al. 2004). Importantly, these traits may be traded against each other (e.g. exploratory behaviour

and ability to cope with social stress in the great tit *Parus major*; Verbeek et al. 1999), such that the evolution of each trait may be constrained by selective pressures acting on other traits. However, so far, most studies have focused on single associations between one behavioural trait and dispersal (Clobert et al. 2009; Cote et al. 2010), ignoring the inter-dependence between these behavioural traits in relation to dispersal. Moreover, selective pressures acting on dispersal at various spatial scales through fitness returns of different life-history strategies may affect the (co-)evolution of behavioural traits (see Réale et al. 2010; Wolf et al. 2007) and their link with dispersal. Therefore, a better understanding of the links between behavioural traits and dispersal, defining dispersal behavioural syndromes, requires simultaneously considering different behavioural traits in the context of dispersal.

In this study, we investigated differences in several behavioural traits between individuals differing in their dispersal propensity and settlement ability in new habitat patches (i.e. colonization ability) to test whether dispersal is associated with behavioural profiles in a patchy population of collared flycatchers *Ficedula albicollis*. We made new forest patches available for breeding to flycatchers by providing nesting sites (artificial nest boxes) close to patches with long-term (> 20 years) established populations and monitored the individuals that settled in these patches in the first year and in subsequent years. In particular, we measured (i) individual aggressiveness towards competitors (response to a simulated intrusion by con- or heterospeifics), (ii) neophobia (response to the presence of a novel object in proximity to the nest) and (iii) risk-taking (response to the presence of a dummy nest predator in proximity to the nest). We then compared the levels (scores) in these behaviours between individuals breeding in new patches (i.e. colonizing individuals) and in patches already present in previous years, and repeated this comparison after two years to control for spatial variation, to test whether colonizing individuals show specific behavioural profiles as a result of dispersal behavioural syndromes in this population. We will present here preliminary comparisons for aggressiveness and neophobia.

Materiel and Methods

Study population and site

The study was done in a patchy population of a small migratory passerine bird, the collared flycatcher (*Ficedula albicollis* Temm.). The collared flycatcher breeds in natural tree cavities but readily accepts artificial nest boxes, which allowed us to manipulate the

availability of breeding sites and create new breeding patches, as well as monitor breeding activity and data. Adults arrive from the wintering grounds from the end of April until the end of May (first two-year-old or older individuals and then yearlings), and the breeding season lasts until the beginning of July. Autumn migration starts from mid-August until mid-September. During the breeding season, adults are sexually dimorphic (black and white plumage for males, brown plumage for females), allowing easy recognition from a distance.

The study site is located in the Southern part of the island of Gotland, Sweden (57°10'N, 18°20E) (Gustafsson 1989; Pärt and Gustafsson 1989) and comprises spatially discrete forest patches separated by non-suitable habitat for reproduction for flycatchers (fields, pastures). In 15 of these patches, 20 to 150 nest boxes (depending on patch size) have been regularly erected (between-box distance of 20-40 m) and have been monitored since the early to mid-80's. Flycatchers compete with other hole-nesting passerines for the access to nest boxes (mainly great tits *Parus major* and blue tits *Cyanystes caeruleus*), with higher competition levels in smaller plots because the proportion of nest boxes occupied by tit species increases with decreasing patch area (unpublished data). More details on the study population and site can be found in Doligez et al. (2004, 2009, 2012), Gustafsson (1989), Pärt and Gustafsson (1989).

Colonisation experiment

In early spring 2011 (beginning of April), 8 new breeding patches were installed in the direct vicinity of the long-term monitored patches, with similar nest box type and density as in these long-term patches. In addition, 3 new patches were installed in early spring 2012. These new patches showed similar environmental characteristics and vegetation than the long-term monitored patches, thereafter called 'old patches'. In 2011, one of the new patches was found to host a relatively important number of collared flycatcher pairs breeding in natural nesting sites (i.e. many birds were present throughout the season but very few nests were found in boxes) and was therefore excluded from the experiment. In 2012, no flycatcher pair settled in one of the new patches, which was therefore also excluded. In total, we monitored colonizing flycatcher individuals in 10 new patches, containing 20 to 60 nest boxes each. The maximal distance between a new and an old patch was less than 1 km (Figure 1).

Nest boxes were installed in the new patches before the arrival of flycatchers. To prevent the settlement of tit species, which could provide social information to arriving flycatchers and decrease the availability of breeding sites, we blocked the entrance hole of the

nest boxes in the new patches until the presence of the first arrived flycatchers was detected over the study site and unblocked nest boxes within the next two days thereafter.

Population monitoring

Each year, all nests boxes were visited regularly (every 2 to 4 days except during incubation) to record detailed breeding data (nest building stages, laying and hatching dates, clutch size, number and condition of nestlings, final number of fledged young). Breeding adults were caught while incubating (for females) and feeding nestlings (for males), identified using individually numbered metal rings, aged (yearling vs. older adults) based on plumage characteristics (Svensson 1992), measured (in particular wing and tarsus length) and weighed. Nestlings were ringed and weighed when day 8 and then measured and weighed again on day 12. Fledging usually occurs on day 16-17. All breeding and individual information is recorded in the long-term data base, allowing us to access to the past dispersal history of individuals in the population. Each year, approx. 40% of adults breeding in the old patches were previously unringed, including a mix of true immigrants and local birds previously missed, especially males. Indeed, capture probability is tightly linked to breeding activity and success in this population and each year, approximately 30% of males remain unidentified in early failed nests.

Behavioural tests

In the year of installation of the new patches (2011-2012) and two years later (2013-2014), behavioural tests were conducted on breeders in both new and old plots to measure several behavioural traits. Here, we analysed measures of levels of aggressiveness and neophobia. All behavioural tests were performed during the morning and late afternoon, i.e. when birds showed highest activity, to maximize the chance of participation to the tests.

Aggressiveness was measured during the nest building phase, i.e. when the risk of losing a nest box to a conspecific competitor was highest in this single-clutch species. Aggressiveness towards conspecific intruders was shown to decrease after the start of incubation (Kral and Bicik 1989; Kral 1996; Kral et al. 1996) even though aggressiveness towards great tit intruders remained high throughout the breeding cycle (Král and Bičík 1992). Aggressiveness was measured here as the response of the focal breeding pair to a simulated intrusion by a conspecific pair. When the nest was half built (i.e. presence of a relatively large amount of nest material in the box but without a nest structure), we placed a

dummy male and female (made of painted clay) on the nest box, one dummy at the entrance hole and the other on the box lid (at random). We used two decoys to elicit and measure an aggressive response by both pair members, even though males are usually more aggressive than females (Boerner and Kruger 2009; Fresneau et al. 2014). In addition to this visual stimulus, male song playback was simultaneously broadcasted from speakers placed just under the nest box (Kral and Bičík 1994). After placing the dummy pair and the speakers at the nest box as quickly as possible (usually within 3 min), the observer hid under a camouflage net at a distance of seven to ten meters away from the box and recorded the behavioural responses of the focal pair during fifteen minutes. The test was repeated twice at two to four days of interval. For the analyses presented here, we used only the data of the first test during which at least one individual responded to the stimulus. For each focal individual, we recorded three behaviours possibly displayed during the test: (i) movements, recording the distance of the individual from the nest box (individual on the nest box, at less than 2 m away from the box, between 2 and 5 m, between 5 and 10 m, or farther than 10 m from the nest box) and time spent in each distance category; (ii) alarm calling, with duration and intensity of alarm calls and (iii) hovering and attacking attempts towards dummies.

Neophobia was measured when nestlings were 5 days old, i.e. during the period when provisioning by parents is highest. Neophobia was measured here as the response of the focal breeding pair to the sudden appearance of a novel object in a familiar environment (Garamszegi et al. 2009; Mettke-Hofmann et al. 2002). We used as a novel object a small coloured figurine (a red and blue hockey player) of approximately 8 cm high. The neophobia test comprised two parts: first, we recorded the behaviour of parents in the absence of change in the environment during one hour; second, we placed the novel object besides the entrance hole of the nest box (within 3 cm of the hole) and recorded the behaviour of parents in presence of the object during one hour. The comparison between the two parts of the test allowed us to measure the change in behaviour due to the presence of the novel object, i.e. the level of neophobia. The tests were video recorded with camouflaged recorders placed at a distance of 6 to 10 m from the nest box depending on the surrounding vegetation. At the start of the test, the observer set up the video recorder before going to the nest box and simulating the placement of the object, so that the perturbation due to the presence of the observer at the nest box was the same between both parts of the test. After one hour of undisturbed recording, the observer came back to the box to place the novel object near the entrance hole. Video recordings were analysed after field work and for each parent, we recorded four behaviours possibly displayed during the test: (i) movements around and on the nest box, (ii) entrances

into the nest box, (iii) hovering over the novel object and (iv) attacks (pecking) towards the object.

Behavioural measures: scores and PCA axes

We explored two different measures of levels of aggressiveness and neophobia: first we scored each behavioural trait and second we used axes of a PC analysis. Aggressiveness score was based on three variables: (i) mean distance from the nest box during the test, weighed by the time spent in each distance category (see above), (ii) whether the individual hovered over the dummies and (iii) whether the individual attacked the dummies. We categorized mean distance based on the data tertiles (less than 4 m, between 4 and 7 m, more than 7 m) and attributed scores of 3, 2 and 1 for each category, respectively. We added 1 to the score if the individual hovered over a dummy and 1 if the individual attacked a dummy. Aggressiveness scores thus varied between 1 and 5. Individuals not observed during the test were not scored because it was not possible to determine whether the individual was not present or was non-aggressive.

Neophobia score was based on four variables: (i) whether the individual returned during the second part of the test, i.e. in presence of the novel object, (ii) whether the individual resumed nestling provisioning, i.e. entered the nest box, during the second part of the test, (iii) the difference in the latency to enter to the nest box between the first and the second part of the test and (iv) the difference in the number of feeding visits (i.e. number of entrances) per time unit after the first entrance (i.e. entrance frequency) between the first and the second part of the test. We attributed a score of 6 to individuals that were present in the first part of the test but not in the second part; a score of 5 to individuals that were present in both parts but did not enter the nest box during the second part; a score of 4 to individuals that entered the nest box in both parts of the test with a difference in entrance frequency between the second and first part of the test < -5 (i.e. a strong reduction in provisioning rate in presence of the novel object); a score of 3 to individuals with a difference in entrance frequency between -5 and 0; a score of 2 to individuals with a difference in entrance frequency > 0 (i.e. no reduction in provisioning rate in presence of the novel object) while showing no aggressive behaviour to the object (i.e. no attacks); and a score of 1 to individuals with a difference in entrance frequency > 0 and that attacked the object. Individuals that were not present or did not enter the nest box during the first part of the test were discarded, because this was supposed to reveal perturbation due to the recording device.

Second, we extracted a response variable for each behavioural trait from a PC analysis, using the first axis of the PCA. For aggressiveness, we included in the PCA the following variables: mean distance from the nest box weighed by the time spent in each distance category, and the hovering and attack rates (i.e. number per min). The mean distance for individuals that were not seen during the test (50 individuals) was fixed to the maximal value (i.e. 10 m). For neophobia, we included in the PCA the following variables: difference in entrance frequency between the two parts of the test, difference in latency to return and enter the nest box between the two parts of the test, and number of attacks towards the novel object. The difference in latency for individuals that did not return during the second part of the test was set to the maximum value, that is the length of the second part of the test minus the latency to return and enter the nest box during the first part of the test. For each behavioural trait, we used as a response variable the first axis of the PCA, which explained 53.1% and 55.7% of the variation in the measures of aggressiveness and neophobia respectively. For aggresiveness, the value of the first axis of the PCA decreases with increasing aggressiveness level as measured by independent behavioural variables, contrary to the value of the score. Conversely, for neophobia, the value of the PCA first axis increases with increasing neophobia level as measured by behavioural variables, as does the score (see supplementary material).

We measured aggressiveness level for 348 individuals (174 of each sex ; 167 different pairs) and neophobia level for 302 individuals (149 for males and 153 for females ; 167 different pairs) in total, in both new and old patches, in the year of installation and two years later.

Statistical analyses

We present here preliminary analyses comparing both response variables (score and PCA axis) for the two behavioural traits (aggressiveness and neophobia) between patch types and years separately, i.e. old vs. new patches in the year of installation; old patches in the year of installation vs. two years later; new patches in the year of installation vs. two years later; and old vs. new patches two years after installation of new patches. Because of limited measures of aggressiveness for individuals in the old patches two years after the new patch installation currently available (extraction of data from audio recordings is currently in progress), our analysis for this trait was limited to the comparisons between old and new patches in the year of installation and between new patches in the year of installation and two years later. We used linear models (continuous response variables) including patch category

(old vs. new patch) or year (year of installation or two years later), as well as sex as explanatory variables. Analyses were performed using the R software (R Core Team 2014).

Results

Aggressiveness

Individuals showed a higher aggressiveness score in the new compared to old patches in the year of installation (estimate ± SE for the old compared to new patches: - 0.43 ± 0.21, $F_{1,198} = 4.276$, P = 0.040) but the value of the first PCA axis did not differ between both patches ($F_{1,198} = 1.152$, P = 0.285). Furthermore, individuals breeding in the new patches were more aggressive during the year of installation than two years later, as measured by both the score (marginally significant difference; estimate ± SE for two years after settlement compared to the year of settlement: - 0.367 ± 0.190, $_{1,208} = 3.733$, P = 0.055) and the value of the first PCA axis (estimate ± SE for the year of settlement compared to two years later: 0.337 ± 0.149, $F_{1,208} = 5.739$, P = 0.017).

In addition, males were more aggressive than females. This was observed for both the score and first PCA axis, and for both comparisons, i.e. when comparing old and new patches in the year of installation (score: estimate ± SE for males compared to females: 1.070 ± 0.202, $F_{1,198} = 28.197$, P < 0.001; PCA first axis: estimate ± SE for females compared to males: - 0.976 ± 0.195, $F_{1,199} = 25.161$, P < 0.001) and when comparing new patches in the year of installation and two years later (score: estimate ± SE for males compared to females: 0.800 ± 0.181, $F_{1,209} = 19.473$, P < 0.001; PCA first axis: estimate ± SE for females compared to males- 0.614 ± 0.141, $F_{1,208} = 18.868$, P < 0.001).

Neophobia

No difference was found in the individual response to the presence of the novel object between old and new patches, either in the year of installation or two years later, whatever the response variable used (score or PCA first axis). Neophobia level did not differ between individuals in old and new patches either in the year of installation (PCA first axis: $F_{1,124} = 0.543$, P = 0.463; score: $F_{1,124} = 0.825$, P = 0.366) or two years later (PCA first axis: $F_{1,172} = 0.031$, P = 0.861; score: $F_{1,172} = 0.834$, P = 0.362). Furthermore, neophobia level did not differ in new patches between the year of installation and two years later (PCA first axis: $F_{1,145} = 1.725$, P =

0.191; score: $F_{1,145} < 0.001$, $P = 0.980$), and it did not differ in old patches between the two time periods either (PCA first axis: $F_{1,152} = 3.491$, $P = 0.064$; score: $F_{1,152} = 3.201$, $P = 0.076$).

Neophobia level was lower for males compared to females in all comparisons between types of plots and time periods, and for both response variables (PCA first axis and score) (Table 1)

Discussion

Because dispersal entails costs (Bonte et al. 2012), natural selection is expected to favour the association between dispersal and traits allowing dispersers to reduce these costs (Clobert et al. 2009). Among these traits, behavioural traits such as aggressiveness and exploration may allow individuals to acquire a breeding site more easily and get familiar with their new environment more rapidly (Cote et al. 2010). This may be particularly crucial in the context of colonization of new habitat patches because individuals may face stronger competition with local heterospecifics and may not have access to social information from conspecifics compared to already occupied habitat patches. Here, we experimentally tested whether individuals colonizing newly installed breeding patches show different behavioural profiles than individuals in already settled populations. Because our new patches were very close to long-term monitored breeding patches in the study site, observed differences would be unlikely to result from spatial differences between individuals or their movement ability. Based on previous studies in other passerine species (Dingemanse et al. 2003; Duckworth and Badyaev 2007), we predicted that individuals colonizing our new patches would be more aggressive and less neophobic than individuals breeding on old patches. Our preliminary results partly confirmed this prediction because individuals colonizing new patches were more aggressive that individuals in old patches and individuals in new patches two years later, controlling for between-sex difference in aggressiveness. However, we found no difference in the level of neophobia between individuals in old and new patches, both in the year of installation and two years later, controlling for between-sex difference in neophobia, although our results should be considered with caution given the preliminary nature of our analyses.

Methodological considerations

As mentioned above, the analyses presented here were a first step to compute and validate responses variable that relevantly measure our behavioural traits, aggressiveness and neophobia, in our study population. We tested two approaches here: (i) a score built by considering a continuous gradation in the aggressive or neophobic response of individuals to the stimuli (see e.g. Bize et al. 2012; Duckworth 2006) and (ii) the first axis of a PCA for a set of behavioural responses potentially reflecting aggressiveness or neophobia levels. Interestingly, our results were very similar with these two measures, yielding the same differences between sexes and nearly the same differences between old and new patches depending on the year in the level of aggressiveness but not neophobia. The PCA first axis of neophobia behaviour explained a large part of the variance in difference of return latency and difference in entrance frequency while the attack rate was almost orthogonal to the first axis, meaning that between-individual variability in attack rate was not considered in this first axis. Computing a score allowed us maximal flexibility, in particular when considering individuals that did not return or to incorporate information on rare events such as attacks. Using scores may thus seem more promising to measure biologically relevant and continuous variation in behavioural profiles of individuals in the field. However, the validation of this measure needs further work to explore the influence of factors already found to relate to aggressiveness and neophobia levels in other populations (such as sex but also age, body condition etc.).

Furthermore, our models were kept simple here. However, all comparisons should be made within a single statistical model, allowing us to test for interactions. Here we expect that individuals colonizing new patches will differ from individuals in old patches but only in the year of installation, because after two years the population should have settled and present the same characteristics than in old plots. This is supported by the net increase in population size between the first and second year, and no further change after two years (unpublished data). Thus we expect to find a significant interaction between the type of patch (new vs. old) and the time period (year of installation vs. two years later). If individuals in new plots were found to show the same increased aggressiveness compared to old plots after two years (which was not tested here), the observed difference in aggressiveness level would not be a consequence of a colonization behavioural syndrome but may simply reflect patch differences. Similarly, a decrease in aggressiveness level in old patches between the year of installation of new patches and two years later would reveal that the decrease in new plots between the two time periods may result from environmental temporal variation. Finally, we accounted here only for sex differences in behavioural responses. But these responses can differ depending on individual's

age and/or previous dispersal history, time in the breeding season or habitat quality. These factors still need to be accounted for in the analyses, as well as the possible dependency of behavioural responses of the male and the female of a nest (nest random effect).

A behavioural syndrome of colonization?

Individuals colonizing new breeding patches may benefit from being more aggressive because they could displace potential heterospecific competitors (Duckworth and Badyaev 2007). Here, collared flycatchers are competing with great and blue tits for the access to breeding sites (Gustafsson 1987). Great tits are 50% heavier and both tit species show higher aggressiveness than flycatchers; therefore they show higher competitive ability, being able to kill flycatchers intruding into their nest box (Merilä and Wiggins 1995). Tits also start breeding on average 2 to 3 weeks before flycatchers and therefore may monopolize breeding sites. For this reason, in a breeding patch where nesting sites are scarce, such as in patches to be colonized in natural situations, it should pay flycatchers to be more aggressive to be able to secure a breeding site. Here, the sudden increase in the availability of breeding sites released this interspecific competitive pressure, but the individuals that explored and settled in new patches should still show behavioural differences associated with colonization ability. In our study, the presence of collared flycatchers is tightly linked to the presence of nest boxes, because natural holes remain limited (pers. obs.; see also Hjernquist et al. 2009), especially in the traditionally managed open forests (*änge*). Therefore, even though we cannot exclude that some of the individuals measured here were already breeding in the new plots in the year(s) before we installed nest boxes, most individuals were likely to be immigrants into these new plots. We also expected colonizing individuals to show lower neophobia level, but we did not find such differences. At this stage, it is not possible to say whether this lack of difference is due to our measures of neophobia not being valid or to a real absence of difference in neophobia level associated with colonizing ability. Aggressiveness and exploration have been reported to positively correlate in another population of collared flycatchers (Garamszegi et al. 2009), although this association may depend on environmental conditions (Garamszegi et al. 2016). More work is needed here to investigate such patterns in our population.

Importantly, we aimed in this study at investigating several behavioural traits simultaneously in association with dispersal and colonization ability (at a small spatial scale), to explore behavioural syndromes associated with dispersal. Indeed, different behavioural traits may be linked by positive or negative associations (Garamszegi et al. 2016), and natural selection may favour associations between traits either directly (if individuals gain fitness

benefits by exhibiting the behavioural trait considered) or indirectly (if individuals gain fitness benefits by exhibiting another behavioural trait correlated to the trait considered). The implications of these two processes can however strongly differ. The first step towards understanding the mechanisms leading to associations between dispersal or colonization ability and other behavioural traits is to measure these behavioural traits simultaneously in different environmental conditions. Once completed, our results should address this question and shed light on multiple dimensions behavioural syndromes associated with dispersal.

This study reports preliminary results about behavioural differences between individuals colonizing new habitat patches and individuals settling in already occupied patches. Much work remains to be done to complete the behavioural measures and test for more complex models, but our results already support such behavioural differences (here in the level of intra-specific aggressiveness). These results provide yet another example of the fact that individuals settling in new habitat patches are not a random sample of a population, with potential consequences on evolutionary processes linked to dispersal (Edelaar and Bolnick 2012). To fully assess the evolutionary consequences of non-random dispersal with respect to behavioural traits in this population, the next step will be to assess the fitness consequences of the associations between dispersal ability and behavioural traits, in varying environmental conditions.

Table 1: Comparison of neophobia behaviour between patch types or years with (a) the first axis PCA variable and with (b) the score, by linear model. In each model, the sex was included as explanatory variable. For each effect, we gave the estimation ± standard error, the degrees of freedom of test F, the F-statistics and the associate p-value.

Variable	Estimation (± s.e.)	df	F	p-value
(a) Neophobia - First axis PCA variable				
Old vs. new patches in the year of installation				
Intercept	- 0.545 (± 0.145)			0.009
Sex (female)	0.687 (± 0.204)	125 ; 1	11,345	0,001
Patch (old)	- 0.151 (± 0.205)	124 ; 1	0.543	0.463
New patches in the year of installation vs. two years later				
Intercept	-0.259 (± 0.150)			0.086
Sex (female)	0.559 (± 0.213)	146 ; 1	7,948	0.006
Year (2013)	0.283 (± 0.215)	145 ; 1	1.725	0.191
Old patches in the year of installation vs. two years later				
Intercept	- 0.037 (± 0.103)			0,717
Sex (female)	0.195 (± 0.204)	151 ; 1	0.916	0,34
Year (2013)	0.385 (± 0,206)	152 ; 1	3,491	0,064
Old vs. new patches two years after installation of new patches				
Intercept	0.142 (± 0.102)			0,166
Sex (female)	0.175 (± 0,204)	173 ; 1	0.732	0,394
Patch (old)	- 0.036 (± 0.204)	172 ; 1	0.031	0.861
(b) Neophobia - Score				
Old vs. new patches in the year of installation				
Intercept	3.641 (± 0.191)			< 0,001
Sex (male)	- 0.802 (± 0.272)	125 ; 1	8.686	0,004
Patch (old)	- 0.248 (± 0.273)	124 ; 1	0.825	0.366
New patches in the year of installation vs. two years later				
Intercept	3.740 (± 0.177)			< 0,001
Sex (male)	- 0.753 (± 0.249)	146 ; 1	9.132	0.003
Year (2013)	- 0.006 (± 0.254)	145 ; 1	0.0006	0.98
Old patches in the year of installation vs. two years later				
Intercept	3.638 (± 0.170)			< 0,001
Sex (male)	- 0.514 (± 0.246)	152 ; 1	4.375	0.038
Year (2013)	0.441 (± 0.247)	151 ; 1	3.201	0.076
Old vs. new patches two years after installation of new patches				
Intercept	3.719 (± 0.159)			< 0,001
Sex (male)	- 0.507 (± 0.227)	173 ; 1	4.984	0.027
Patch (old)	0.208 (± 0.227)	172 ; 1	0.834	0.362

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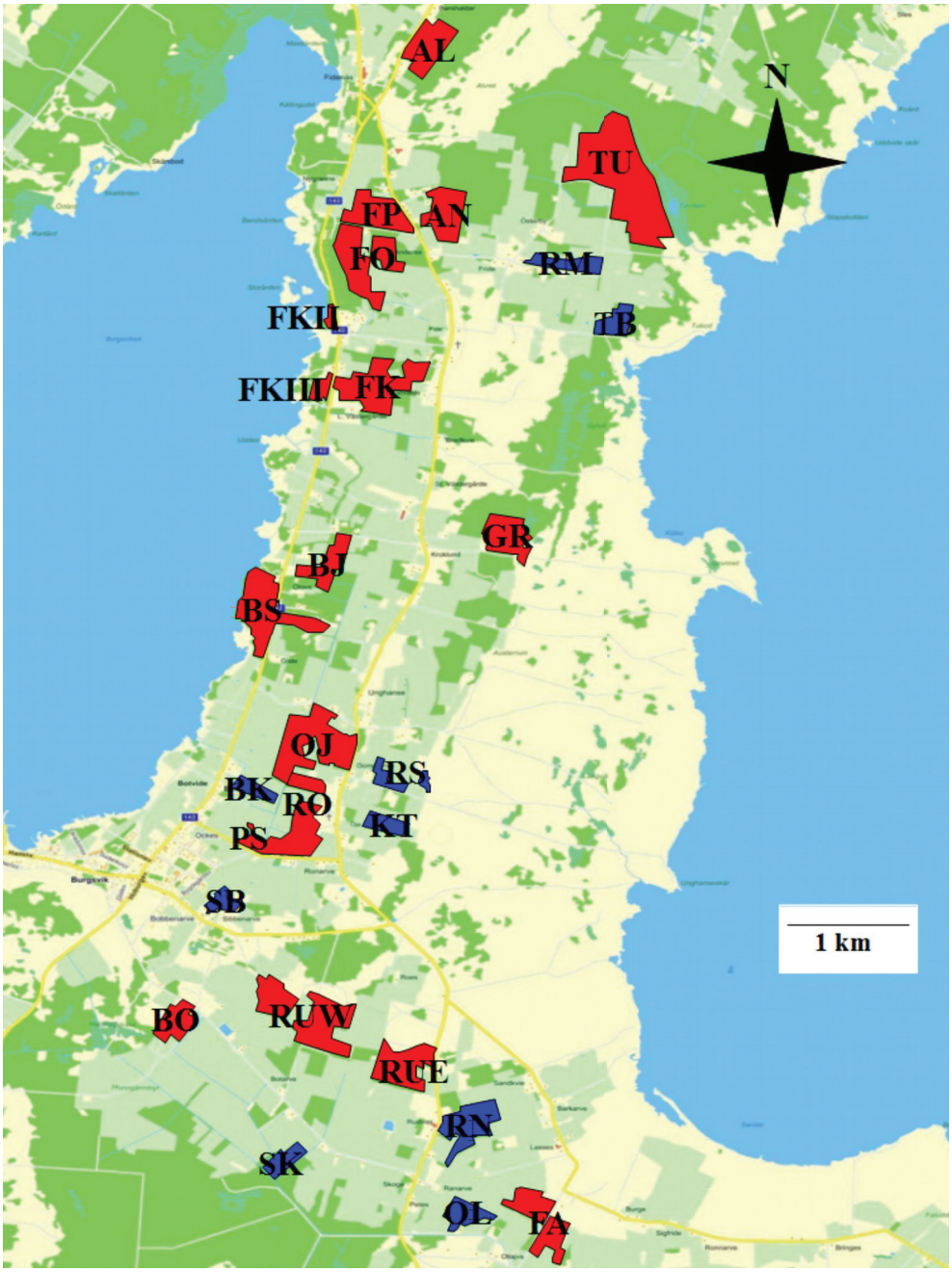
Figure Legned

Figure 1 : Map of the study site in the south part of Gotland island with the old patches (in red) and new patches (in blue). Each patch is identified by a name, reduced to a short name on this map.



Discussion Générale et Perspectives

Au cours de ce travail, nous avons tenté de montrer non seulement la base génétique de la dispersion, condition indispensable à l'évolution de ce trait d'histoire de vie, mais aussi les corrélations phénotypiques et génétiques entre dispersion et traits comportementaux, et ainsi mettre en évidence des syndromes comportementaux de dispersion pouvant influencer sur l'évolution de la dispersion au sein d'une population.

Rappel des résultats

Les résultats du présent travail de thèse tendent à montrer que les individus qui dispersent ne sont pas une part aléatoire de la population, mais des individus avec des caractéristiques particulières.

Tout d'abord, nous avons montré que, dans notre population d'étude de gobe-mouches à collier, il existe une base génétique du comportement de dispersion, tant pour la dispersion natale ($h^2 = 0,37$), que pour la dispersion globale,qui regroupe les événements de dispersion natale et de reproduction ($h^2 = 0,22$). Par ailleurs, nous avons mis en évidence que l'héritabilité de la dispersion natale est plus importante que l'héritabilité de la dispersion globale, comme nous pouvions nous y attendre. Cela peut s'expliquer par le fait que les adultes ayant déjà fait au moins une reproduction ont intégré leur propre expérience dans leur choix de disperser ou non les années suivantes. De plus, nous avons montré que les variables environnementales représentant la qualité de l'habitat impactent significativement la dispersion des individus que ce soit pour la dispersion natale ou de reproduction.

Enfin, un des résultats notables est la variable spatiale (le bois de départ pour l'année considérée) qui, quand elle est intégrée aux modèles, est non seulement importante (entre 19 % et 26 % de la variance phénotypique totale), mais surtout qui prélève une part de la variance génétique additive. Ce faisant, elle conduit l'estimation de l'héritabilité de la dispersion dans notre population à décroître (dispersion natale : de 0,37 à 0,10 ; dispersion globale : de 0,22 à 0,06). Ceci nous incite à penser à l'existence d'une structuration spatiale génétique de notre population, même si la ou les causes de cette structuration spatiale restent à déterminer.

Dans le second chapitre, nous avons pu montrer que dans les populations considérées de martinets à ventre blanc, non seulement la dispersion natale des individus est héritable

(h^2=0,56), mais que le comportement de défense du nid l'est aussi dans une moindre mesure (h^2=0,16).

De plus, nous avons mis en évidence tant une corrélation phénotypique que génétique entre ces deux traits, ce qui nous conduit à l'idée que ces deux traits sont intégrés fonctionnellement pour donner ce qui est défini comme un syndrome comportemental de dispersion. La relation négative entre dispersion natale et comportement de défense du nid peut être la conséquence soit de la sélection directe sur le comportement de défense du nid, soit de la sélection d'un autre trait lui-même corrélé à la dispersion et au comportement de défense du nid.

Enfin, dans le troisième chapitre, nous avons testé la présence d'un syndrome comportemental de dispersion dans notre population de gobe-mouches à collier. Pour cela, nous avons conduit une expérience de colonisation, en mesurant les niveaux d'agressivité et de néophobie dans les bois nouvellement installés et les bois suivis à long terme.

Nous avons pu mettre en évidence une corrélation phénotypique positive entre le niveau d'agressivité des individus et la colonisation d'un milieu nouvellement disponible. Les individus qui se sont installés dans les nouveaux bois sont plus agressifs comparativement aux individus qui se sont reproduits dans les bois suivis à long terme. Par ailleurs, le niveau d'agressivité des individus dans ces nouveaux bois a diminué si nous comparons l'année de colonisation et la deuxième année suivant cette colonisation. Des analyses statistiques supplémentaires et plus poussées sont néanmoins nécessaires pour confirmer ce que nous avons mis en évidence. En effet, nous ne pouvons actuellement savoir si ce que nous avons trouvé est le résultat de la présence d'un vrai profil colonisateur dans notre population ou bien dû à un effet lié au bois (spatial) ou à l'année (temporel).

En ce qui concerne la néophobie par contre, aucune corrélation avec la colonisation du nouveau milieu n'a pu être mise en évidence. Cela va à l'encontre de notre prédiction, à savoir que les individus dispersants devraient montrer un niveau de néo-phobie plus faible que les individus non-dispersants. Une étude plus poussée est nécessaire, afin savoir si cette première conclusion est juste ou si c'est la conséquence d'une mauvaise mesure du comportement de néophobie.

Discussion générale

Les preuves que le comportement de dispersion, trait d'histoire de vie clé pour les dynamiques de population et les flux de gènes, a une base génétique, s'accumulent. En effet, des études portant sur d'autres espèces d'oiseaux, ont aussi reporté des niveaux d'héritabilité, faibles à modérés, de la dispersion (e.g. Charmantier et al. 2011 ; Hansson et al. 2003 ; Korsten et al. 2013 ; Pasinelli et al. 2004 ; Wheelwright and Mauck 1998). Les estimations peuvent notamment varier en fonction des méthodes utilisées (Régression parent/jeune ou modèles animaux ; Charmantier et al. 2011; de Villemereuil et al. 2013; Doligez et al. 2012), mais aussi du type de comportement de dispersion étudié. Au sein d'une même espèce, la dispersion natale est très souvent plus importante que la dispersion de reproduction (Paradis et al. 1998). Ici, non seulement la dispersion natale est plus importante que la dispersion de reproduction, mais la dispersion natale présente également des niveaux d'héritabilité plus importants que la dispersion globale, cette dernière incluant les événements de dispersion natale et de dispersion de reproduction. Donc, l'ajout des événements de dispersion de reproduction fait baisser l'estimation de l'héritabilité de la dispersion dans notre population. La différence d'héritabilité estimée entre ces deux types de dispersion peut s'expliquer par le fait que les individus qui se sont déjà reproduit au moins une fois, peuvent intégrer à leur décision de disperser ou non l'expérience de leurs précédentes reproductions, informations auxquelles les recrues d'une population n'ont pas accès directement.

De plus, l'importance de la part environnementale dans la variance phénotypique totale de la dispersion (e.g. cette thèse, Korsten et al. 2013), même si la nature exacte de la variance environnementale reste à déterminer, indique que la dispersion, bien que basée génétiquement, reste un trait très plastique. La base génétique de la dispersion nous rappelle néanmoins que, malgré la plasticité de la dispersion, tous les individus ne peuvent pas avoir un comportement de dispersion optimale en fonction de conditions environnementales données.

Au delà de l'impact de l'environnement sur la dispersion, l'importance des facteurs internes sur la dispersion des individus n'est pas à ignorer. La dispersion peut être liée à un ensemble de traits phénotypiques corrélés entre eux, formant un syndrome de dispersion. Dans cette thèse, nous avons pu montrer que la dispersion est liée négativement tant phénotypiquement que génétiquement à un comportement. La démonstration d'une telle corrélation génétique, entre dispersion et comportement, vient se rajouter aux études de Duckworth and Kruuk (2009) et de Korsten et al. (2013). L'existence de telles corrélations peut s'expliquer par le fait que le comportement aide à la dispersion en réduisant les coûts qui

y sont associés lors d'une ou plusieurs phases de la dispersion. Dans notre cas, les individus dispersants présentent un niveau de défense du nid (face à un potentiel prédateur) plus faible que les individus philopatriques, c'est à dire qu'ils vont avoir tendance à s'envoler rapidement dès la vue d'un potentiel prédateur. Or, durant la phase de transfert de la dispersion, où l'individu se déplace entre deux sites, les risques de prédation peuvent être accrus (Belichon et al. 1996 ; Waser et al. 1994). Être réactif à l'approche d'un potentiel prédateur peut donc être un avantage durant cette phase pour réduire les risque de prédation.

La dispersion de ces individus peut aussi être seulement la conséquence de leurs caractéristiques comportementales. En effet, dans le contexte de colonies avec de fortes densités de population, des individus qui sont moins enclins à défendre leur nid pourraient aussi présenter un niveau d'agressivité moindre envers les intrusions. L'hypothèse d'un possible lien entre témérité et agressivité n'est pas nouvelle et a déjà été testé dans plusieurs études (Barnett et al. 2012 ; Pintor et al. 2008 ; Verbeek et al. 1996). Dans notre cas, les individus moins téméraires et moins agressifs pourraient alors subir la contrainte de la compétition entre individus de la même espèce plus fortement que les individus capables de défendre leur territoire efficacement. Les individus moins agressifs seraient donc probablement plus sujets à la dispersion dans une autre colonie que les individus plus agressifs s'imposant dans leur colonie d'origine, afin de pouvoir se reproduire. La persistance d'une telle corrélation entre dispersion et comportement de défense de nid au sein de cette populations d'individus philopatriques peut être favorisée dans le cas de variabilités spatio-temporelles de l'habitat, permettant par exemple la repopulation de colonies ayant subit une forte baisse démographique.

Cependant, l'agressivité qui peut favoriser la philopatrie dans un contexte de forte densité, peut aussi se retrouver être un avantage lors de la dispersion et notamment dans le cas de la colonisation d'un nouveau milieu, en facilitant l'installation dans un nouveau site. Nos résultats du troisième chapitre tendent à montrer une corrélation positive entre dispersion et agressivité, ce qui va dans le même sens que l'étude de Duckworth and Badyaev (2007) chez le merle bleu. Finalement, le sens des corrélations entre dispersion et comportement peut être variable selon les espèces considérées et leur caractéristiques écologiques. Actuellement, nous n'avons pas de prédictions théoriques sur quelles associations de traits (agressivité et néophobie par exemple) attendre selon les espèces, selon qu'elles soient longévives ou non, qu'elles soient coloniales ou non ou encore qu'elles soient migratrices ou non. De même, nous ne savons pas à quelles associations nous attendre selon les conditions environnementales. Il serait donc intéressant que les travaux futurs cherchent à comprendre l'influence de ces

facteurs (conditions environnementales et caractéristiques des espèces) pour prédire le sens et la nature des associations attendues entre comportements.

Perspectives

Les études ayant montré une corrélation génétique entre dispersion et comportement (Duckworth and Badyaev 2007; Korsten et al. 2013), incluant celle sur le martinet à ventre blanc du chapitre 2, ne s'intéressent qu'à un seul trait comportemental (agressivité, exploration ou défense du nid). Bien que permettant de mettre en évidence des syndromes comportementaux de dispersion, elles ne prennent pas en compte les possibles corrélations avec d'autres traits comportementaux. Il se peut qu'il y ait des associations (positives ou négatives) entre traits comportementaux. Les pressions de sélection pourraient alors agir indirectement sur l'un ou l'autre de ces traits, c'est à dire via une action sur un trait auxquels ils sont corrélés. Donc il faut non seulement s'intéresser à comprendre les associations entre les différents traits comportementaux et la dispersion, mais aussi entre les traits comportementaux entre eux, afin d'avoir une meilleure idée des associations sur lesquelles se fait réellement la sélection, et lesquelles sont simplement conséquentes à la sélection sur un autre trait corrélé et qui ne sont donc pas sous sélection directe elles-mêmes.

Dans le chapitre 1, nous avons vu qu'une partie de la variance additive génétique de la propension à disperser chez le gobe-mouche à collier était prise par la variance liée à la fragmentation de l'habitat. L'une des hypothèses pour expliquer ce phénomène est qu'il existe une certaine héritabilité de la sélection de l'habitat dans notre population, c'est à dire que les individus choisissent leur site de reproduction en fonction de signaux ou d'indices dont l'utilisation est génétiquement déterminée. La sélection d'un nichoir par un individu dans notre population est notamment influencée par l'utilisation de l'espace par la mésange charbonnière. Rechercher, par exemple, s'il existe des différences héritables dans la manière dont les individus appréhendent ce signal serait une des clés pour comprendre pourquoi, dans notre population, les individus apparentés, qui ont la même tendance à disperser, partagent aussi le même environnement.

De plus, l'utilisation de l'information pourrait être un mécanisme pour expliquer l'intégration fonctionnelle de la dispersion avec les traits comportementaux. En effet, si les traits comportementaux peuvent influencer l'utilisation de l'information dans la prise de décision (e.g. Kurvers et al. 2010), et que cette même prise de décision est liée aux décisions

de dispersion, alors l'évolution du comportement de dispersion ne serait qu'un sous-produit de la sélection sur la sélection de l'habitat. Il serait donc utile de déterminer si l'utilisation de l'information est héritable et si elle est corrélée (phénotypiquement et génétiquement) à des traits comportementaux, pour mieux appréhender les mécanismes proximaux à la base des syndromes comportementaux de dispersion.

Ce travail de recherche et les résultats qui en découlent (ainsi que les résultats à venir) apportent leur contribution à la mise en évidence et à la quantification du déterminisme génétique de la dispersion et des syndromes comportementaux liés à la dispersion impliquant un ensemble de traits comportementaux (agressivité, néophobie, témérité), ainsi que leurs conséquences sur l'évolution de la dispersion au travers des associations entre ces traits.

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ANNEXES

ANNEXE 1

Food supplementation mitigates differences in nest-defence behaviour between dispersing and non-dispersing individuals in a passerine bird

Charlotte Récapet, Grégory Daniel, JoëlleTaroni, Pierre Bize* and BlandineDoligez*

Submitted

Food supplementation mitigates differences in nest-defence behaviour between dispersing and non-dispersing individuals in a passerine bird

Charlotte Récapet, Grégory Daniel, JoëlleTaroni, Pierre Bize* and BlandineDoligez*

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Abstract

Dispersal behaviour is a major response to environmental spatio-temporal variability and has been shown to be associated with individual variation in behavioural and life-history traits. However, to what extent these differences between dispersing and non-dispersing individuals are fixed or depend on external conditions remain poorly known. To explore such differences, we manipulated local habitat quality by providing additional food during the nestling feeding period in a patchy population of collared flycatchers and we compared nest defence against a dummy predator between dispersing and non-dispersing parents at the end of the experiment. Dispersing birds showed more intense nest defence behaviour in supplemented compared to control nests, whereas non-dispersing birds showed a strong response in both treatments. These effects were independent of brood value. This difference may result from a dispersal cost, with dispersers being normally constrained to invest more in foraging behaviour, and supplementation releasing this constraint. It may also reflect two distinct behavioural strategies associated with dispersal in this population, with dispersers adjusting their investment when breeding in low-quality habitat while non-dispersers show a less flexible reproductive investment. Experimentally testing the influence of environmental variation in behavioural and life-history responses of dispersing and non-dispersing individuals therefore needs more attention when assessing the costs and benefits of dispersal.

1. Introduction

Dispersal, defined as the movement of individuals between breeding sites or between the birth site and the site of first breeding [1], is a fundamental process in ecology, allowing rapid individual responses to environmental variation, in particular the deterioration of local conditions [2]. Dispersal decision are mainly driven by an interaction between environment and condition, but recent studies in different taxa have shown that dispersal propensity is partly heritable [3–5]. One explanation for the maintenance of this loss of flexibility in dispersal is that natural selection might favour the functional and genetic integration of dispersal with various phenotypic traits that reduce dispersal costs [6,7]. This has led to the hypothesis that dispersal would be associated with fixed differences in behavioural and physiological traits, defining a "dispersal syndrome" [6,8]. In particular, boldness toward predators and exploratory tendency are the behavioural traits most consistently associated with dispersal [9,10] (but see [11]). However, natural selection is also expected to favour flexibility, to better adjust to external conditions, rather than fixation of behavioural traits. Thus, an alternative explanation is that dispersing individuals differ in their response to environment and that observed variation would be conditional on the environment rather than fixed [12].

To explore whether differences between dispersing and non-dispersing individuals were fixed or conditional on environmental conditions, we manipulated habitat quality by providing additional food during the nestling rearing period in a patchy population of collared flycatchers *Ficedula albicollis*. Just before fledging, we measured nest defence behaviour against a natural nest predator, the red squirrel, in individuals that previously bred in the patch and in new comers, while controlling for brood value.

2. Material and methods

The study was conducted in spring 2014 on a patchy population of collared flycatcher breeding in nest boxes on the island of Gotland, Sweden (57°07'N, 18°20'E).

Nest boxes in our eight experimental plots were monitored regularly throughout the season to record breeding data (hatching dates, brood size, mass and tarsus length of nestlings on day 12). Parents were caught inside boxes, aged (yearlings vs. older adults) based on plumage

characteristics [13] and previous capture history, and weighed when chicks were six to 12 days old. Dispersal was defined as a change of breeding patch between birth and the first capture as a breeder (natal dispersal) or between successive captures as a breeder (breeding dispersal). Non-dispersing individuals did not change plot between successive captures (see [14] for a discussion of this binary definition of dispersal in the collared flycatcher). We excluded all previously unringed adults, which were of uncertain dispersal status because a fraction of local breeders are missed every year.

Food availability was manipulated by providing additional food to half of our nests (N = 86 supplemented nests) from day two to day 12 post-hatching. 30g of live maggots were provided once a day, between 07:00 and 19:00, in transparent containers attached to nest boxes. Control nests (N = 82) received no food, but were visited daily to be subjected to the same level of disturbance. Treatments were assigned to nests randomly by blocks accounting for hatching date and plot to control for spatio-temporal variation. The natural variation in habitat between plots was controlled for by measuring breeding density on available nest boxes, which is well correlated with breeding success in our population [15], but could also reflect varying levels of competition.

Nest defence was measured when chicks were 13-days old by placing a stuffed red squirrel on the entrance of the nestbox, mimicking a nest predator attack on nestlings. To avoid premature fledging, nestbox entrance was closed during the test. The stuffed squirrel was left for no longer than 5min from the arrival of the second parent and no longer than 15 min from the observer's arrival. If no adult was seen, it was removed after 10min. An observer hidden under a camouflage net and sitting at least 10 meters from the nestbox recorded the behaviour of the pair. Recorded behaviours are described in Table S1. Because some parents arrived less than 5 min before the end of the test, only behavioural responses during the 4.5min following an individual first sighting were available for all individuals and used in the analyses. One individual that arrived only 16s before the end of the test was considered absent during the test. Following an exploratory multivariate analysis of the behavioural data (Supplementary material S1), a nest defence score was computed based on the behaviours that best described the intensity of the response: the time spent within 2 meters of the box, the number of moves, and the presence/absence of direct attacks to the dummy (Table 1).

Table 1: Construction of the nest defence score. The cut-off values for the two quantitative variables are the tertiles in the whole population.

<table>
<tr><td colspan="2" rowspan="2">Not seen: 0</td><td colspan="3">Time spent within 2m of the nest box</td><td></td></tr>
<tr><td>t ≤ 29.9%</td><td>29.9% < t ≤ 81.1%</td><td>t > 81.1%</td><td></td></tr>
<tr><td rowspan="3">Activity = number of moves</td><td>a ≤ 14</td><td>1</td><td>2</td><td>3</td><td rowspan="3">If at least one attack or swoop:</td></tr>
<tr><td>14 < a ≤ 26</td><td>2</td><td>3</td><td>4</td></tr>
<tr><td>a < 26</td><td>3</td><td>4</td><td>5</td></tr>
<tr><td></td><td></td><td colspan="3">If at least one attack or swoop:</td><td>+1</td></tr>
</table>

We obtained 67 females (25 dispersing, 42 non-dispersing) and 61 males (10 dispersing, 51 non-dispersing) from 101 different nests, for whom both dispersal status and nest defence behaviour were known. The supplemented (N = 51) and control nests (N = 40) differed neither in brood size at the beginning of the treatment (Wilcoxon rank-sum test: W = 886, P = 0.257) nor in laying date (W = 903, P = 0.35).

We investigated the effect of the interaction between the supplementation treatment, breeding density, and dispersal status on individual nest defence score using a linear mixed-effects model. We included sex, age, body mass, brood size, and average nestling body mass as fixed covariates in interaction with the treatment and nest and observer as random effects to control for the non-independence of the two pair members and for variation between observers. To test whether we measured nest defence on a biased sample of breeders, we investigated the effects of the supplementation treatment, the dispersal status, and their interaction on the probability of total brood failure, on brood size, and on average nestling body mass (with average tarsus length as covariate), on males and females separately. Non-significant effects (starting with interactions) were removed based on type-III F-tests with denominator degrees of freedom calculated using Satterthwaite's approximation (R package 'lmerTest' [16]).

3. Results

The mean (± SE) nest defence score was 2.9 ± 1.7, and it varied between 0 and 6. Nest defence score differed between dispersing and non-dispersing individuals and this difference depended on the food supplementation treatment (interaction dispersal status by supplementation treatment: $F_{1,108} = 3.95$, P = 0.049, Figure 1). In control nests, dispersing birds had a lower score than dispersing ones (post-hoc test: -1.32 ± 0.48, $F_{1,50} = 7.61$, P =

0.008), whereas the score of non-dispersing and dispersing birds did not differ anymore in supplemented nests (-0.30 ± 0.39, $F_{1,68}$ = 0.57, P = 0.45). The difference between dispersing and non-dispersing individuals also depended on breeding density ($F_{1,106}$ = 6.38, P = 0.01): nest defence decreased with density in dispersing birds (-3.65 ± 1.62, F1,21 = 5.11, P = 0.03) but not in philopatric birds (+1.73 ± 1.13, $F_{1,85}$ = 2.34, P = 0.13). There was an interaction between brood size and treatment ($F_{1,61}$ = 4.10, P = 0.047): the nest defence score tended to increase with brood size in control nests (+0.23 ± 0.12, $F_{1,49}$ = 3.42, P = 0.07), but not in supplemented nests (-0.09 ± 0.14, $F_{1,43}$ = 0.38, P = 0.54). Individual's age, either alone or in interaction with dispersal, body mass and sex had no effect on nest defence score (all P > 0.18, Table S3).

The probability of total brood failure between the start of the treatment and the nest defence test was lower in males from supplemented nests, although not significantly so in females (GLM with a binomial error distribution; females: -0.78 ± 0.43, $F_{1,100}$ = 3.27, P = 0.07 ; males: -1.48 ± 0.63, $F_{1,76}$ = 6.19, P = 0.02). Brood failure was independent of dispersal (females: $F_{1,99}$ = 0.22, P = 0.64; males: $F_{1,75}$ = 0.46, P = 0.50), and its interaction with the supplementation (females: $F_{1,98}$ = 3.04, P = 0.08; males: $F_{1,74}$ = 0.0002, P = 0.99). Brood size during the test was higher in supplemented nests (females: +1.16 ± 0.40, $F_{1,65}$ = 8.31, P = 0.005; males: +1.23 ± 0.39, $F_{1,59}$ = 9.90, P = 0.003), but independent of dispersal (females: $F_{1,64}$ = 0.36, P = 0.55; males: $F_{1,58}$ = 0.06, P = 0.81) or its interaction with the supplementation (females: $F_{1,63}$ = 1.19, P = 0.28; males: $F_{1,57}$ = 0.57, P = 0.45). Nestling body mass was higher when the parents were dispersers, although no significantly so for males (females: +0.52 ± 0.24, $F_{1,64}$ = 4.83, P = 0.03; males: +0.72 ± 0.36, F1,58 = 3.91, P = 0.052) There was no effect of supplementation (females: $F_{1,63}$ = 0.07, P = 0.80; males: $F_{1,57}$ = 0.81, P = 0.37), or its interaction with dispersal (females: $F_{1,62}$ = 0.88, P = 0.35; males: $F_{1,56}$ = 1.37, P = 0.25).

4. Discussion

Dispersing individuals increased the intensity of nest defence when food availability was increased compared to control conditions. In contrast, non-dispersing individuals showed a high intensity of nest defence whatever the treatment. Consistently, food abundance was positively linked to nest defence in Ural owls [17] and great tits [18], controlling for brood size. There was no evidence of a bias in our sample due to lower success of a non-random fraction of individuals, since the probability of breeding failure before the test did not depend on the interaction between supplementation and dispersal. Intra-individual flexibility rather

than inter-individual differences might therefore explain a large part of the observed variation in nest defence behaviour.

The parental investment theory postulates that parental care should increase with current reproductive value, which increases with nestling number and condition, and decrease with residual reproductive value, which represents the future breeding prospect of the individual [19]. Here, we found no strong effect of brood size or nestling mass, reflecting current reproductive value, or of parent age or body mass, possibly reflecting residual reproductive value, on nest defence behaviour. The variation in nest defence behaviour was thus not mediated by differential effects of the supplementation on nestlings survival and growth, or on adult condition.

The observed difference between dispersing and non-dispersing birds could result either from a constraint on, or from an adaptive adjustment by, dispersers. In control conditions, dispersing individuals may not be able to invest as much time and energy in nest defence as non-dispersing individuals. They may indeed not be able to exploit their habitat as efficiently due to unfamiliarity [20] and need to reallocate time and energy to foraging and nestling provisioning. However, when such constraint is released, here food supplementation, dispersing individuals can increase their investment in other parental care behaviours, such as nest defence. Under this hypothesis, the reduced nest defence in control nests would reflect a cost in terms of immediate increased risk of nest predation. Alternatively, our results could suggest the existence of different investment strategies, with dispersing individuals adjusting their level of parental care depending on resource availability while non-dispersing ones show a constantly high investment in nest defence. Under this hypothesis, the reduced nest defence behaviour in control nests would reflect a beneficial adjustment by dispersing individuals. Consistently, variation in nest defence seems beneficial to dispersing individuals, as nestlings body mass was higher for dispersing parents. Our study population is characterised by a low level of nest predation compared to other similar passerine populations, thanks to the absence of mustelid species on Gotland [21]. Because the most important factor determining reproductive success is the availability of resources for nestlings, selection may have favoured high investment in nestling provisioning at the expense of other parental behaviours.

In conclusion, this study experimentally shows the role of environment in mediating differences in behaviour during breeding between dispersing and non-dispersing individuals. Description of dispersal syndromes that do not take environmental variability into account might thus be intrinsically flawed and to better understand the processes at play on the

evolution of dispersal strategies, we encourage integrating measures of habitat quality or manipulating it when studying behavioural syndromes, but also differences in life-histories, associated to dispersal.

Ethics statement. Permission for catching, ringing and providing additional food to adult and young birds was granted by the Ringing Centre from the Museum of Natural History in Stockholm (licence number 471:M009 to CR).

Data accessibility. Data will be available from the Dryad Digital Repository.

Authors' contributions. CR, GD, BD and PB designed the study; CR, JT and GD carried out the field work; JT extracted the data from the tests recordings; CR and JT analysed the data; CR, PB and BD drafted the manuscript. All authors gave final approval for publication. The authors hereby declare that they have no competing interests.

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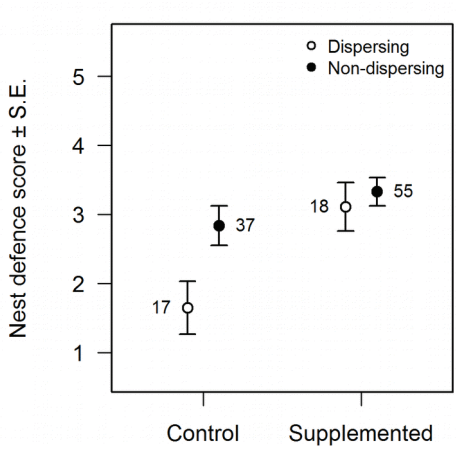

Figure 1: Effect of the food supplementation treatment on the nest defence score of dispersing and non-dispersing individuals.

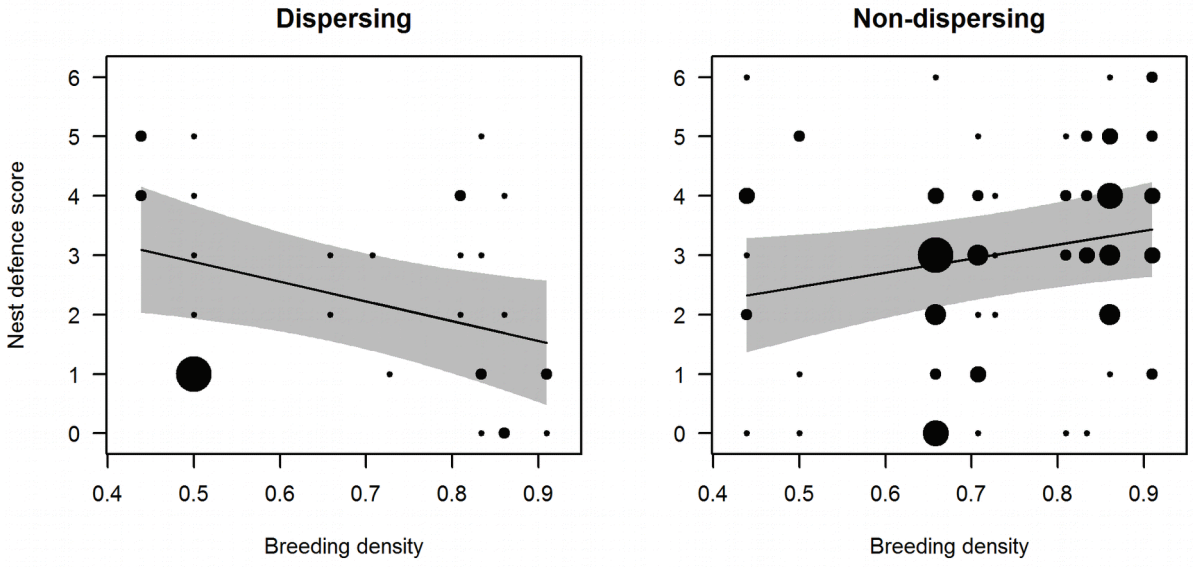

Figure 2: Effect of the breeding density on the nest defence score of dispersing and non-dispersing individuals.

Supplementary Table S1: Ethogram used to code the behavioural tests. Alarm calls were also frequent, but could rarely be attributed to one of the parents, especially when these remained far from the nest box. They were therefore not included in the score.

Behaviour	**Description**
+ 10 meters	The bird flies and lands more than ten meters from the nest box or out of view.
- 10 meters	The bird flies and lands between ten and five meters from the nest box.
- 5 meters	The bird flies and lands between five and two meters from the nest box.
- 2 meters	The bird flies and lands within two meters of the nest box.
Attack	The bird attacks the dummy squirrel by giving it a peck.
Hovering	The bird does a stationary flight in front of the nest box.
Swooping	The bird plunges toward the dummy squirrel to chase it.

Supplementary information S2: Comparison of the nest defence score with a Principal Component Analysis of behaviour

Excluding whose individuals that were not seen during the test, and one individual that arrived 16s before the end of the test, a Principal Component Analysis was performed on the following behavioural variables (function dudi.pca of the 'ade4' package1):

- latency between the start of the test and the bird's arrival
- time spent within 2 meters of the nest
- time spent within 5 meters of the nest, but further than 2 meters
- time spent within 10 meters of the nest, but further than 5 meters
- time spent alarming
- activity = number of moves
- number of attacks and swooping (cf. Supplementary Table S1).

The first principal component explained 33.4% of the variance in behaviour. This figure dropped to 17.9% for the second component. The loadings of the first principal axes showed that the latency and alarms did not contribute much to this axis. Moreover, alarms contributed positively to the first axis and were negatively correlated to activity and the time spent within 2 meters, as did the time spent within 5 meters and within 10 meters. The intensity of the nest defence response was thus best described by the time within 2 meters, the activity, and the attacks. As the correlation coefficients between these three variables were moderate, we kept them all to build the nest defence score.

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Loadings (Correlations)	Principal axis 1	Principal axis 2
Latency	0.041 (0.063)	-0.102 (-0.114)
Time within 2 meters	-0.553 (-0.846)	-0.419 (-0.469)
Time within 5 meters	0.348 (0.533)	0.552 (0.618)
Time within 10 meters	0.387 (0.591)	0.048 (0.053)
Alarms	0.293 (0.448)	-0.372 (-0.416)
Activity	-0.489 (-0.748)	0.367 (0.411)
Attacks and swooping	-0.309 (-0.473)	0.483 (0.541)

	Time within 2 meters	Time within 5 meters	Time within 10 meters	Alarms	Activity	Attacks and swooping
Latency	0.014	0.074	-0.062	-0.086	-0.115	-0.099
Time within 2 meters		-0.651	-0.556	-0.173	0.431	0.121
Time within 5 meters			-0.031	0.048	-0.132	-0.118
Time within 10 meters				0.159	-0.316	-0.072
Alarms					-0.346	-0.171
Activity						0.458

Using the first Principal Component as a response variable instead of the calculated score yielded similar results, although the power was lower due to the individuals excluded (Supplementary Table S3).

The probability not to be seen during the test (including the late individual) could not be properly modelled due to the low number of individuals concerned. However, it followed a similar pattern with a higher proportion of missed individuals in dispersing birds from control nests compared to philopatric birds or dispersing birds from supplemented nests:

Treatment	Control		Supplemented	
Dispersal status	Dispersing	Philopatric	Dispersing	Philopatric
Absent:Present (Proportion)	3:14 (0.18)	5:32 (0.14)	1:17 (0.06)	3:52 (0.05)

Using the score thus paper allowed us to include these individuals in the analyses, while maintaining the contribution of the three major variables. The distribution of the score was as follow:

Score	0	1	2	3	4	5	6
N	12	19	16	30	24	21	5

Supplementary Table S3: Linear mixed-effect model best describing the sources of variation in nest defence score (white cells), and non-significant marginal effects (grey cells). A similar model was then applied to the score and the first Principal Component for individuals present during the test. The sample size and the partition of the random variance are given beside each model. The initial full model included age, sex, brood size during the test, adult body mass, average body mass of nestlings, and their interaction with the supplementation.

Effect	Estimate ± S.E.	F	Num. d.f.	Den. d.f.	P
Nest defence score $V_{residual}$ = 1.97 (N = 127 adults), V_{pair}= 0.24 (N = 91 pairs), $V_{observation}$ = 0.31 (N = 3 experimenters)					
Brood size	0.26 ± 0.12	0.79	1	60.05	0.378
Breeding density	1.61 ± 1.15	0.62	1	70.34	0.435
Dispersal	1.88 ± 1.35	3.46	1	97.04	0.066
Supplementation	1.92 ± 0.91	7.61	1	62.24	0.008
Brood size x Supplementation	-0.37 ± 0.18	4.10	1	60.98	0.047
Dispersal x Breeding density	-4.70 ± 1.86	6.38	1	106.28	0.013
Dispersal x Supplementation	1.20 ± 0.60	3.95	1	108.27	0.049
Age class (Yearlings)	0.83 ± 0.62	1.79	1	112.13	0.183
Age class (Yearlings) x Suppl.	0.90 ± 1.21	0.56	1	111.81	0.456
Sex (Males)	0.11 ± 0.27	0.18	1	59.64	0.677
Adult body mass	-0.06 ± 0.22	0.07	1	115.20	0.795
Nestlings average body mass	0.01 ± 0.10	0.01	1	57.01	0.915
Nest defence score (excl. absent individuals) $V_{residual}$ = 1.35 (N = 115 adults), V_{pair}= 0.25 (N = 84 pairs), $V_{observation}$ = 0.42 (N = 3 experimenters)					
Brood size	0.18 ± 0.11	0.90	1	65.73	0.346
Breeding density	1.01 ± 1.01	0.03	1	75.20	0.864
Dispersal	0.21 ± 1.20	0.43	1	93.87	0.514
Supplementation	0.97 ± 0.82	3.50	1	69.45	0.066
Brood size x Supplementation	-0.21 ± 0.16	1.58	1	67.03	0.213
Dispersal x Breeding density	-2.32 ± 1.70	1.86	1	99.23	0.176
Dispersal x Supplementation	1.15 ± 0.55	4.40	1	96.66	0.038
First Principal Component (opposite to homogenize the signs) $V_{residual}$ = 1.20 (N = 115 adults), V_{pair}= 0.41 (N = 84 pairs), $V_{observation}$ = 0.45 (N = 3 experimenters)					
Brood size	0.23 ± 0.12	0.53	1	74.05	0.468
Breeding density	1.18 ± 1.02	0.29	1	82.39	0.593
Dispersal	0.93 ± 1.21	1.37	1	98.98	0.244
Supplementation	1.59 ± 0.83	5.97	1	77.26	0.017
Brood size x Supplementation	-0.34 ± 0.17	3.96	1	75.21	0.050
Dispersal x Breeding density	-3.30 ± 1.71	3.73	1	102.58	0.056
Dispersal x Supplementation	0.96 ± 0.55	2.99	1	100.87	0.087

ANNEXE 2

Estimation and comparison of heritability and parent–offspring resemblance in dispersal probability from capture–recapture data using different methods: the Collared Flycatcher as a case study

Blandine DOLIGEZ[1*], Grégory DANIEL[1], Patrick WARIN[2,3], Tomas PÄRT[4], Lars GUSTAFSSON[5] and Denis RÉALE[6]

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ORIGINAL ARTICLE

Estimation and comparison of heritability and parent–offspring resemblance in dispersal probability from capture–recapture data using different methods: the Collared Flycatcher as a case study

Blandine Doligez · Grégory Daniel · Patrick Warin · Tomas Pärt · Lars Gustafsson · Denis Réale

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Abstract Understanding the evolution of a trait requires analysing its genetic basis. Many studies have therefore estimated heritability values of different traits in wild populations using quantitative genetic approaches on capture–recapture data of individuals with known parentage. However, these models assume perfect individual detection probability, a hidden hypothesis that is rarely met in natural populations. To what extent ignoring imperfect detection may bias heritability estimates in wild populations needs specific investigation. We give a first insight into this question using dispersal probability in a patchy population of Collared Flycatchers *Ficedula albicollis* as an example. We estimate and compare heritability and parent–offspring resemblance in dispersal obtained from (1) quantitative genetic approaches ("classical" parent–offspring regressions and more recent animal models) and (2) multi-state capture–recapture models accounting for individual detection probability. Unfortunately, current capture–recapture models do not provide heritability estimates, preventing a full comparison of results between models at this stage. However, in the study population, detection probability may be expected to be lower for dispersing compared to philopatric individuals because of lower mating/breeding success and/or higher temporary emigration, making the use of capture–recapture models particularly relevant. We show significant parent–offspring resemblance and heritable component of between-patch dispersal probability in this population. Accounting for imperfect detection does however not seem to influence the observed pattern of parent–offspring resemblance in dispersal probability, although detection probability is both sensibly lower than 1 and heterogeneous among individuals according to dispersal status. We discuss the problems encountered, the information that can be derived from, and the constraints linked to, each method. To obtain unbiased heritability estimates, combining quantitative genetic and capture–recapture models is needed, which should be one of the main developments of capture–recapture models in the near future.

Keywords Capture–recapture models · Family effects · Individual detection probability · Mixed models · Quantitative genetics

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B. Doligez (✉) · G. Daniel
CNRS; Université de Lyon, 69000 Lyon; Université Lyon 1, France. Department of Biometry and Evolutionary Biology, CNRS UMR 5558, Bâtiment Gregor Mendel, 43 boulevard du 11 novembre 1918, 69622 Villeurbanne cedex, France
e-mail: doligez@biomserv.univ-lyon1.fr

P. Warin
Commissariat à l'Energie Atomique (CEA), INAC, SP2M, NM, UMR-E 9002, 17 rue des martyrs, 38054 Grenoble, France

P. Warin
Université Joseph Fourier, SP2M, UMR-E 9002, 38041 Grenoble, France

T. Pärt
Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, 750 07 Uppsala, Sweden

L. Gustafsson
Department of Ecology and Genetics/Animal Ecology, Evolutionary Biology Centre, University of Uppsala, Norbyvägen 18D, 752 36 Uppsala, Sweden

D. Réale
Department of Biological Sciences, Université du Québec à Montréal, Case postale 8888, succursale centre-ville, Montréal, QC H3C 3P8, Canada

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Introduction

The response of a trait to evolutionary pressures directly depends on its heritability and the strength of the selective pressures acting on this trait. Understanding the evolution of a trait in natural populations therefore involves analyzing (1) the variation in this trait among individuals, (2) the relationship between this trait and individual fitness, and (3) the genetic basis of the trait (Fairbairn and Reeve 2001; Kruuk et al. 2008). Based on capture–recapture data collected over generations, many evolutionary studies have used quantitative genetic models to estimate heritability of morphological, physiological, behavioral and life-history traits and address related evolutionary questions in natural populations (reviews in, e.g., Kruuk et al. 2008; Stirling et al. 2002). In particular, the use of generalized linear mixed models ("animal models") in this context, which allow partitioning the total observed phenotypic variance among individuals between genetic, environmental and other factors by incorporating pedigree information of marked individuals in a population (Kruuk 2004), has recently expanded over classical regressions between close relatives.

However, current quantitative genetic models, developed for captive animal populations, rely on the hidden assumptions that detection and/or capture of individuals is perfect and thus that phenotypic variance is identical among marked and unmarked individuals (Cam 2009). Both hypotheses are unlikely to be met in natural populations (Cam 2009; Clobert 1995; Lebreton et al. 1992), where detection and/or capture probability often depends on individual phenotype such as morphology, behavior (e.g., breeding behavior: Gustafsson and Pärt 1990; or personality: Biro and Dingemanse 2009), health status (e.g., Hawley et al. 2007), etc. Violating the hypothesis of a perfect individual detection can, however, not only lead to biased estimates of the demographical parameters of interest but also to flawed inferences on the biological processes revealed by relationships between these estimates and other factors, as shown for survival patterns (see, e.g., Gimenez et al. 2008; Martin et al. 1995). This issue can therefore not be ignored (Cam 2009). Capture–recapture (CMR) methods have been specifically developed to account for imperfect individual detection and its heterogeneity among individuals, but they remain largely ignored in the context of estimating trait heritability (Cam 2009). However, classical CMR models do not currently allow random effects, which could include genetic effects from pedigree information, to be tested and therefore cannot directly estimate heritability levels. Building the required CMR mixed models (Cam 2009) or "capture–recapture animal models" (O'Hara et al. 2008; Papaïx et al. 2010) by integrating random effects while accounting for imperfect detection has only been undertaken very recently (Papaïx et al. 2010; Royle 2008).

Until CMR mixed models become fully available, the question remains to what extent ignoring imperfect individual detection probability may bias heritability estimates in wild populations. In order to explore this question, we attempted here to compare measures of heritability (i.e., the fraction of additive genetic variance in the total observed phenotypic variance for a trait) or parent–offspring resemblance (i.e., the degree by which offspring trait is affected by parental trait) obtained via methods accounting (CMR models) and not accounting (quantitative genetic models) for imperfect detection for a given behavioral trait. As an example, we used on the one hand classical parent–offspring regressions and animal models, and on the other hand CMR models to estimate heritability of, or parent–offspring resemblance in, dispersal probability in a patchy population, in order to highlight the constraints linked to each method. Dispersal, defined as the movement of an individual from its natal or previous breeding site to a new breeding site (Greenwood and Harvey 1982), is a key life-history trait for evolutionary biology, ecology and conservation biology (Clobert et al. 2001; Kokko and López-Sepulcre 2006; Ronce 2007). Dispersal strategies have been found to evolve in response to selective pressures in the wild (Duckworth and Badyaev 2007; Kokko and López-Sepulcre 2006; Thomas et al. 2001), suggesting a genetic basis of dispersal. Evidence for heritability of dispersal traits has been found mainly in plants and insects, in particular with selection experiments on seed or pollen dispersal structures or wing morphology (Roff and Fairbairn 2001; Ronce 2007). In vertebrates, direct evidence supporting a genetic basis of dispersal traits is rare (Sinervo and Clobert 2003; Trefilov et al. 2000; see also Dingemanse et al. 2002; Roff and Fairbairn 2001 for selection experiments on exploratory or movement traits), but indirect evidence is accumulating in the form of within-family (sibling and parent–offspring) resemblance in dispersal behavior (reviews in Doligez and Pärt 2008; Massot and Clobert 2000; see also Massot et al. 2003; Sharp et al. 2008).

However, all studies providing estimates of dispersal heritability in natural populations so far have completely ignored the issue of imperfect individual detection probability, even when the observed number of recruits was explicitly noted to be much lower than expected (see, e.g., Hansson et al. 2003, in which the authors estimate that 37% of expected recruits were not detected). To what extent these dispersal heritability estimates may be biased thus needs to be explored. Strong biases may be expected because detection probability is likely to differ between dispersing and non-dispersing individuals due in particular to differences in (1) future dispersal probability, and thus

chances to temporarily leave the study area (Doligez and Pärt 2008), and/or (2) breeding status, in particular mating success (e.g., Bensch et al. 1998; Pärt 1994). Accordingly, dispersing individuals may be expected to show lower detection probability, and estimations of dispersal heritability may be affected not only by imperfect individual detection but also by the heterogeneity of detection probability among individuals depending on the trait of interest, here dispersal status, and other traits linked to dispersal (e.g., sex and age; Greenwood and Harvey 1982).

Using dispersal probability, i.e., the probability to disperse to a new habitat patch, we obtained measures of dispersal heritability and parent–offspring resemblance in dispersal in a patchy and unsaturated population of Collared Flycatchers *Ficedula albicollis*, and we compared the results obtained using the same data with different methods. In a first step, we estimated parent–offspring resemblance in between-patch dispersal propensity and heritability using quantitative genetic methods (parent–offspring regressions and animal models). In a second step, we used a multi-state CMR approach to estimate the level of parent–offspring resemblance in between-patch dispersal propensity. In this case, using parental dispersal status as individual initial state (i.e., at age 0), parent–offspring resemblance was estimated via the transition probability between states from age 0 to 1. A full comparison of the three currently available methods is difficult because they yield different kinds of estimates: current CMR models estimate offspring dispersal probability according to parental dispersal status but provide no heritability estimate, while the reverse is true for animal models. The two types of estimates are of course linked (the higher the heritability level, the higher the parent–offspring resemblance) but cannot be directly compared as such. Results from CMR and animal models were therefore both compared to parent–offspring regressions. We discuss the constraints of each method and stress the need for developing CMR mixed models that can be used to estimate heritability of many quantitative and discrete traits in the wild (see O'Hara et al. 2008).

Methods

Study area and study species

The Collared Flycatcher is a short-lived hole-nesting migratory passerine bird. The data were collected between 1980 and 2005 in a spatially patchy population breeding on the island of Gotland, southern Baltic (57°10′N, 18°20′E), where artificial nest boxes were erected in 14 discrete forest plots of varying size (patches) (see Doligez et al. 2009 and Appendix for more details). Each year, adult flycatchers breeding in nest boxes were trapped (females during incubation, males during nestling feeding), identified with individually numbered aluminium rings, and aged (yearlings versus older individuals; Doligez et al. 2009). Breeding data were monitored throughout the season and all nestlings in boxes were ringed. For more details on the study population and study area, see Doligez et al. 2009; Gustafsson 1989; Pärt 1990; Pärt and Gustafsson 1989.

Definition of dispersal, dispersal variables and individual detection probability

Dispersal was defined as an observed change of patch between the years of birth and first breeding (natal dispersal) or between breeding years (breeding dispersal) (Doligez et al. 2009). This binary definition (dispersal versus philopatry) minimizes methodological problems compared to a continuous variable such as dispersal distance, since the array of observable dispersal distances is strongly constrained in this patchy population with respect to settlement decisions at the patch scale (Doligez and Pärt 2008; Doligez et al. 2004; Appendix). Furthermore, this binary variable was found to respond to many social and environmental factors in previous studies on this population (Doligez et al. 1999, 2002, 2004; Doncaster et al. 1997). Only adults whose natal or previous breeding site was known were included in the analyses: unringed immigrants in the study area (on average 35% of breeding adults each year; Doligez et al. 2004) were discarded because these birds include a mix of true immigrants and local birds previously missed. All recruits involved in cross-fostering experiments were discarded from the analyses. Because we focused in this study on comparing the results obtained using different methods rather than obtaining the most precise heritability estimates, we ignored all maternal and environmental factors potentially affecting dispersal in order to keep results fully comparable between methods.

We used for parental dispersal status either the parents' status in the year of offspring birth whatever parents' age (i.e., mixing natal dispersal for first-time breeders and breeding dispersal for older parents) or parental natal dispersal status only (i.e., in the year of offspring birth for first-time breeders or before for older parents). Approximately 15% of nestlings distributed over 33% of nests are extra-pair in this population (Sheldon and Ellegren 1999). Because extra-pair paternity was not determined routinely in this population, and because such levels of extra-pair paternity were shown to have little impact on heritability estimates both using parent–offspring regressions and animal models (Charmantier and Réale 2005; Merilä et al. 1998), we used the dispersal status of the social father.

In this population, the capture of adults is tightly linked to their sex, breeding status and success (see Appendix). As a consequence, dispersal status was in some cases determined with one (30.5%), two (7.4%) or three (1.3%) years of gap (Doligez et al. 2009). In the study population, earlier results suggested that dispersing individuals achieved lower mating and breeding success (Pärt 1991, 1994) and were more likely to subsequently disperse out of the study area (Doligez et al. 1999; Pärt and Gustafsson 1989) than philopatric individuals. Thus, they may be expected to show lower individual detection probability.

Parent–offspring regressions

We first investigated the relationship between dispersal status (disperser versus philopatric individual) of male and female parents and their offspring, controlling for offspring sex, using generalized linear mixed models (GLMMs with binomial error structure and logit link; glimmix macro in SAS; Littell et al. 1996). Offspring dispersal status was determined upon first encounter of individuals as breeders, i.e., we analyzed offspring natal dispersal. Furthermore, because 31% of nests (303 of 974) recruited more than one young, and 51% of recruited offspring (702 of 1,373) were therefore not independent, the models included nest of origin as a random variable to account for the non-independence of siblings.

The heritability (h^2) of a given trait is computed as the ratio of additive genetic variance (σ_A^2) over total phenotypic variance (σ_P^2), and can be estimated by the slope (b) of the corresponding parent–offspring regression (Falconer and Mackay 1996). Estimates of heritability of dispersal probability (binary variable) and associated standard errors were obtained here using the threshold model (Falconer and Mackay 1996). This model assumes that the determination of the variation in a binary trait is the consequence of an underlying character (liability) that is itself continuously distributed. Individuals for which the liability character is below (with respect to above) a threshold value will develop the first (with respect to the second) morph of the dimorphic trait. Because the liability is continuously distributed, the threshold model allows obtaining heritability estimates using the usual linear approach, by linking the heritability measured on a binary (0,1) scale ($h_{0,1}^2$) to the heritability on the underlying continuous scale (h^2) (see Roff 1997; Doligez et al. 2009 for more details). We computed two sets of heritability estimates using parent–offspring regressions considering (1) parental dispersal status in the year of offspring birth, and (2) parental natal dispersal only, independently of the year when it occurred. To account for sibling non-independence in these estimations, we randomly selected one recruit for each breeding attempt that recruited several young, computed heritability estimates on the data subset, and repeated the operation 100 times to obtain mean values of heritability and standard error over the 100 repetitions. Heritability estimates were corrected by the level of phenotypic correlation of dispersal status between parents (Falconer and Mackay 1996; Roff 1997; see Doligez et al. 2009).

Animal models

Animal models are mixed models partitioning the observed total phenotypic variance in a trait (σ_P^2) into additive genetic, parental and environmental components of variance, using information about the degree of relatedness between individuals contained in their pedigree (Kruuk 2004 and references therein). These models consider additive genetic value of individuals as a random effect because they aim at providing an estimate of the variance of this effect rather than one parameter for each individual (Kruuk 2004). In the simplest form of animal models, the phenotype y of individual i can be written as: $y_i = \mu + a_i + e_i$, where μ is the population mean, a_i is the additive genetic value of individual i and e_i is a random residual error (μ is thus the only fixed effect). Random effects a_i and e_i are assumed to have a zero mean and unknown variance to be estimated, σ_A^2 (the additive genetic variance) and σ_R^2 (the residual variance), respectively. If the only random effect in the model is the additive genetic effect, the total phenotypic variance for the trait y is: $\sigma_P^2 = \sigma_A^2 + \sigma_R^2$. Variance components are estimated by fitting the respective random effects in a generalized linear mixed model, and the heritability of trait y is computed as $h^2 = \sigma_A^2/(\sigma_A^2 + \sigma_R^2)$ (Kruuk 2004). In addition to the additive genetic variance (random effect), we included sex and age (fixed effects) in our animal models. In a first analysis, the estimation of heritability of dispersal probability included all dispersal events, thus mixing natal and breeding dispersal events. In a second analysis, only natal dispersal events were analyzed, thus estimating heritability of natal dispersal probability. In the study population, the pedigree depth (i.e., maximum possible number of ancestor generations for an individual) is 25 generations since individuals can start breeding at age 1 (parentage relationships between individuals were unknown in the first year of the study as none were ringed).

The models were run using MCMCglmm, a recently issued R package for fitting generalized linear mixed models using Monte Carlo Markov chain techniques (Hadfield 2010). The model was fitted as if the dispersal variable was normally distributed and thus heritability values were obtained using the threshold model again to transform heritability on the binary (0,1) scale ($h_{0,1}^2$) given by the MCMCglmm package into heritability on the underlying continuous scale (h^2) as above (further work is

needed to run a model fitting directly binary variables using MCMCglmm). Based on the results obtained with parent–offspring regressions, a prior of 0.4 was used for heritability to start with. To compute the posterior mode, the 15,000 first iterations were discarded and 1 iteration was kept every 50 iterations over the next 50,000 iterations (i.e., 1,000 iterations were used in total), in order to reduce autocorrelation between iterations used. The trace and densities of fixed and random effects and residuals were checked. The estimates obtained were similar for different priors tested, indicating that they were not sensitive to the prior chosen. MCMCglmm provides 95% credible interval around each estimate of variance, heritability and fixed effects, allowing testing the significance of these parameters.

Multi-state capture–recapture models: capture histories, effects modeled and notations

Individual capture histories were built using three different events (Pradel 2005): 0, not encountered; 1, philopatric status (i.e., encountered in the same patch as previously); and 2, dispersing status (i.e., encountered in a different patch). Since only individuals born on the study area were included, the first encounter for each individual always corresponded to age 0. Since individual dispersal status was not defined at age 0, the corresponding event was the dispersal status of the same-sex parent. Subsequent events were defined by the dispersal status of the individual. Individual sex and dispersal status of the opposite-sex parent were coded as groups (i.e., 4 groups). Capture histories contained 25 events corresponding to the 26 years of the study considered, excluding the first year for which parental dispersal status was unknown for all individuals. We used E-SURGE (Choquet et al. 2009; Pradel 2005) to estimate survival (S), capture (P) and between-state transition (T) probabilities depending on sex (s), age (a), parental (pd) and individual (id) dispersal status. Parent–offspring resemblance in dispersal probability was estimated through the influence of parental dispersal status on the first between-state transition (age 0 to age 1), separating the dispersal status of same-sex (spd) and opposite-sex (opd) parents. We considered three age classes: yearlings [or age 0 to age 1 for survival S and transition T parameters; $a(1)$], 2-year-old individuals [or age 1 to age 2; $a(2)$] and 3-year-old or older individuals [or after age 2; $a(3)$]. Here, we ignored temporal variations in parameters in order to keep the number of parameters tractable and obtain parameter estimates. Furthermore, year effects when implemented in animal models were very weak (unpublished results).

Because family (random) effects cannot be included in current CMR models, we used an indirect approach to investigate the impact of the non-independence of sibling recruits on model selection. In a first step, we analyzed all recruits (thus with non-independent individuals for nests having recruited several siblings). In a second step, we analyzed 10 of the 100 data subsets created for parent–offspring regressions by randomly selecting one recruit for each nest having recruited several siblings (thus with independent individuals only). The 10 repetitions were chosen to explore the range of heritability values obtained using parent–offspring regressions. Model selection may indeed be expected to differ when estimated heritability values are high and low (i.e., for high and low expected parent–offspring resemblance, respectively). We therefore analyzed the restricted datasets for which estimated heritability was the lowest (three sets) and highest (three sets), closest to the mean value (two sets), and intermediate in the lowest (one set) and highest half of values (one set) (Appendix). We then compared the models selected for the restricted datasets (with one recruit per nest) and the full recruit dataset. We conducted this comparison only for the data with parental dispersal status in the year of offspring birth here, but it could be extended to the data with parental natal dispersal status. See Doligez et al. 2009 for further discussion about other sources of data non-independence (e.g., presence of the same parents in different years).

The validity of the starting models was checked in U-CARE using GOF tests for multi-state capture–recapture data (Choquet et al. 2005; Pradel et al. 2003, 2005). These tests examine (1) whether past encounter history affects the future of individuals when released in the same conditions (test 3G), and in particular transience (effect of past capture; test 3G.Sr) and memory (effect of past state; test WBWA) processes, and (2) whether being caught at occasion t affects the future of individuals (test M), and in particular short-term trap-dependence (effect on capture probability in the next occasion $t + 1$; test M.ITEC) (Pradel et al. 2005). Model notation was extended from Lebreton et al. 1992 and Nichols and Kendall 1995. Model selection was performed using E-SURGE (Choquet et al. 2009) and was based on quasi-Akaike Information Criteria corrected for small sample size (QAICc; Anderson and Burnham 1994). We started from model $S_{s\times a(2,3)\times id}$ $T_{s\times[a(1)\times sdp\times opd+a(2,3)\times id]}$ $P_{s\times a\times id}$ (53 parameters), which included full sex and age effects, dispersal status of both parents on the first transition parameter (age 0 to age 1) and individual dispersal status thereafter on all parameters, down to the simplest, constant model, testing intermediate models including additive effects. Juvenile survival (from age 0 to 1) was here fixed to 1 in all analyses, since only recruits, i.e., individuals surviving up to at least age 1, were considered. However, the total number of models to be tested in this case was above 10^5. Therefore, in order to reduce the number of models, we used a simplified "step-

down" procedure: first, we selected models on capture probabilities while keeping the original parametrization of survival and transition probabilities; second, we simplified survival probabilities using the parametrization of capture probabilities selected in the first step; and, finally, we simplified transition probabilities using the parametrization of survival probabilities selected in the second step (see Doherty et al., this volume, for a discussion about the validity of such a model selection procedure). Models with QAICc of less than five units difference with the best model were kept during the temporary steps of model selection in order to avoid excluding potentially good candidate models. Because we aimed here at comparing the level of parent–offspring resemblance in dispersal propensity obtained using CMR models and parent–offspring regressions, we did not present here the full model selection but focused on the best models selected.

Results

Parent–offspring regressions

Dispersal status of both parents significantly influenced offspring natal dispersal probability in the subsequent year(s). Offspring dispersal probability was higher for dispersing compared to philopatric parents (Fig. 1, white bars; Appendix), both when considering parental dispersal status in the year of offspring birth ($F_{1,404} = 20.47$, $P < 0.0001$ and $F_{1,404} = 14.10$, $P = 0.0002$ for maternal and paternal status, respectively) and parental natal dispersal status ($F_{1,171} = 17.03$, $P < 0.0001$ and $F_{1,171} = 6.61$, $P = 0.011$ for maternal and paternal status, respectively), accounting for offspring sex in each case. When considering parental dispersal status in the year of offspring birth, offspring subsequent dispersal probability was highest when both parents were dispersers, leading to a significant interaction between maternal and paternal dispersal status ($F_{1,404} = 9.30$, $P = 0.0024$).

When considering parental dispersal status in the year of offspring birth, the estimated heritability level of dispersal was 0.30 ± 0.07 (not different between father–offspring and mother–offspring regressions; Doligez et al. 2009). When considering parental natal dispersal status, estimated heritability level was higher: 0.47 ± 0.10 (again, not different between father–offspring and mother–offspring regressions) (Table 1; see Doligez et al. 2009 for further details).

Animal models

Animal models confirmed a significant heritability of dispersal when discriminating genetic from other effects (parental and environmental effects combined). When all dispersal events were considered (i.e., combining natal and breeding dispersal), the additive genetic and residual variances (95% CI) were 0.024 (0.020–0.029) and 0.186 (0.180–0.191), respectively, corresponding to a heritability value h^2 of 0.19 (0.16–0.21) (Table 1). When only natal dispersal events were considered, the additive genetic and residual variances were 0.053 (0.042–0.064) and 0.166 (0.155–0.176), respectively, corresponding to a heritability value h^2 of 0.39 (0.31–0.47) (Table 1). In both cases, males had a lower dispersal probability compared to females, and in the first case, dispersal probability decreased with age. Importantly, the global heritability levels were not fully identical in parent–offspring regressions and animal models. In parent–offspring regressions, this global level corresponded to regressions of offspring natal dispersal status on a mixture of parental natal and breeding dispersal status, while in animal models, it corresponded to a mixture of natal and breeding dispersal heritability. Natal dispersal heritability estimates were however directly comparable with both methods.

CMR models: GOF tests, selected models and parameter estimates

GOF tests

The global GOF tests were highly significant for all datasets (full recruit datasets with parental dispersal status in the year of offspring birth and parental natal dispersal status and 10 restricted subsets to test the effect of sibling non-independence): $845.2 < \chi^2 < 2{,}123.2$, $232 < df < 332$, all $P < 0.001$. This was due to strong apparent transience (test 3G.Sr: $479.4 < \chi^2 < 1{,}210.3$, $42 < df < 46$, all $P < 0.001$) and, to a lesser extent, immediate trap-dependence effects (test M.ITEC: $35.6 < \chi^2 < 63.0$, $26 < df < 40$, all $P < 0.02$ except for the data with parental natal dispersal status: $P = 0.10$). The WBWA ("memory") tests were not significant ($9.67 < \chi^2 < 32.71$, $27 < df < 38$, all $P > 0.71$). However, these apparent transience and trap-dependence effects were probably artificial, due to the way the datasets were built: taking into account recruits only eliminates transients by definition. The current multi-state GOF tests may therefore not be fully adapted to our data. When GOF tests were performed on the same datasets in which the first capture for each individual was deleted, all tests became non-significant for both the data with parental dispersal status in the year of offspring birth (general GOF test: $\chi^2 = 146.7$, $df = 184$, $P = 0.98$; test 3G.Sr: $\chi^2 = 38.3$, $df = 43$, $P = 0.68$; test M.ITEC: $\chi^2 = 15.8$, $df = 18$, $P = 0.60$) and data with parental natal dispersal rate (general GOF test: $\chi^2 = 89.3$, $df = 129$, $P = 0.99$; test

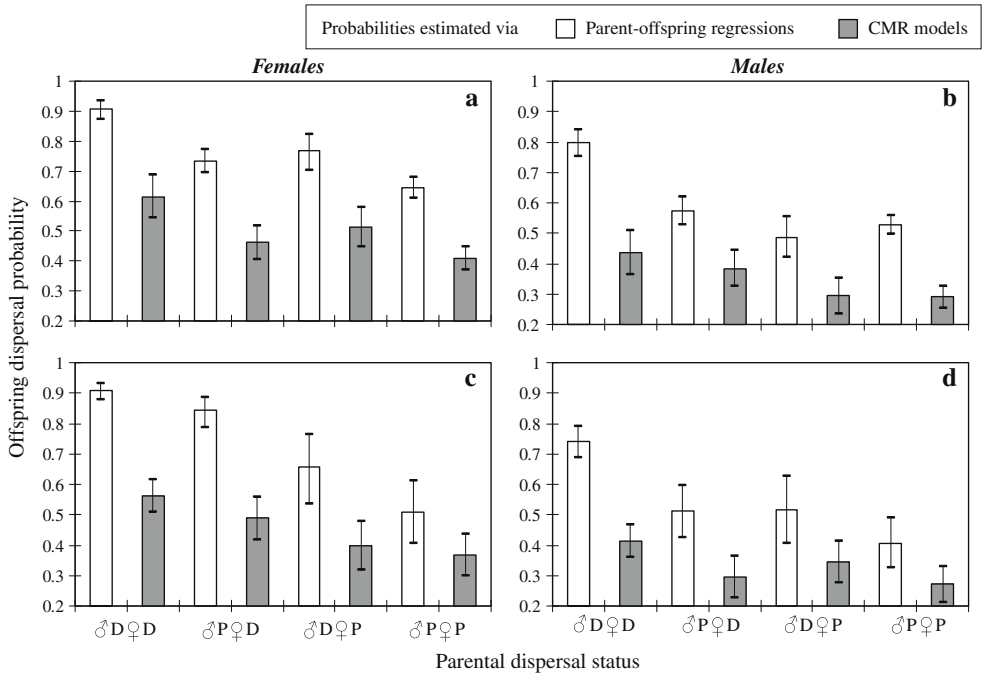

Fig. 1 Offspring dispersal probabilities (±1 SE) according to parental dispersal status obtained via parent–offspring regressions (*white bars*) and CMR models (*gray bars*), for females (**a**, **c**) and males (**b**, **d**). **a**, **b** Parental dispersal status in the year of offspring birth; **c**, **d** parental natal dispersal status. *D* Dispersing parent, *P* philopatric parent. Parameter estimates for CMR models come from the selected model $S_{a(2,3)\times id}\ T_{a(1)\times sdp\times opd\ +\ a(2,3)\times id+sdp/id\times s}\ P_{s+a\times id}$

Table 1 Comparison of dispersal heritability estimates obtained via parent–offspring regressions and animal models, using the threshold model (Falconer and Mackay 1996; see Roff 1997 and Doligez et al. 2009 for more details)

Model	$h^2_{0,1}$	CI($h^2_{0,1}$)	h^2	CI(h^2)
Global heritability level: p(disp) = 0.30				
Parent–offspring regression	0.19	0.10–0.27	0.30	0.16–0.44
Animal model	0.12	0.10–0.13	0.21	0.17–0.23
Natal dispersal alone: p(disp) = 0.60				
Parent–offspring regression	0.29	0.17–0.41	0.47	0.28–0.66
Animal model	0.24	0.19–0.29	0.39	0.31–0.47

$h^2_{0,1}$ (with respect to h^2) is the heritability measured on the 0,1 scale (with respect to the underlying continuous scale), CI are the associated 95% confidence intervals. p(disp) is the proportion of dispersing individuals in the population used to compute h^2

3G.Sr: $\chi^2 = 37.1$, $df = 40$, $P = 0.60$; test M.ITEC: $\chi^2 = 9.9$, $df = 14$, $P = 0.77$; full recruit data in both cases). For this reason, and because apparent transience is taken into account by including an age effect in our models, we proceeded with model selection by correcting QAICc values by the overdispersion parameter $\hat{c} =$ (general GOF test − 3G.Sr test)/remaining df (Pradel et al. 2005). Here, $\hat{c} = 3.19$ and 1.93 for the data with parental dispersal status in the year of offspring birth and parental natal dispersal rate, respectively.

Model selection and parameter estimates for full recruit datasets

Several best models were selected on the full recruit data with parental dispersal status in the year of offspring birth and parental natal dispersal status, but their structure was very close in all cases (Table 2). Transition probability between age 0 and 1 depended on the interaction between the dispersal status of both parents and subsequent transition probabilities depended on the dispersal status of the individual, with an addititional interaction between sex and dispersal status in both cases: $T_{a(1)\times sdp\times opd+a(2,3)\times id+sdp/id\times s}$ (note that *sdp* and *id* correspond to the dispersal status in the capture history at different ages: age 0 for *sdp* and subsequent ages for *id*). The model without dispersal status of the opposite-sex parent could, however, not be excluded for the data with parental natal dispersal status ($T_{a(1)\times sdp+a(2,3)\times id+sdp/id\times s}$; QAICc = 2,508.8 and 2,507.0 for the two models, respectively; Table 2). In all cases, as for parent–offspring regressions, offspring dispersal probability was higher for dispersing compared to philopatric parents (Fig. 1, gray bars; Appendix) and higher for female compared to male offspring. In the case of parental dispersal status in the year of offspring birth, the dispersal status of the opposite-sex parent seems to affect offspring dispersal probability more than the same-sex parent, which leads to the interaction between the dispersal status of the two parents.

Survival probability depended on the interaction between dispersal status and age (2 year-old versus older, juvenile survival *a(1)* being in this case fixed to 1): $S_{a(2,3)\times id}$ (Table 2). However, survival rate of philopatric individuals between age 1 and 2 was non-estimable (fixed to 1), while the other three values were similar. However, forcing survival to depend on age and dispersal status in an additive way, or deleting one or the other effect, strongly increased model QAICc. Therefore, we kept the selected parametrization for survival here. When the first observation for each individual was deleted, the selected model included a constant survival (although models with age or dispersal status alone could not be excluded). The reason for survival probability of philopatric individuals between age 1 and 2 being non-estimable in the general models is not clear and needs further exploration. It should, however, not affect the results since model selection and parameter estimates for transition and capture probabilities were little affected by survival parametrization (results not detailed here).

As expected, detection probability strongly depended on dispersal status in addition to sex and age: $P_{s+a\times id}$ for the data with parental dispersal status in the year of offspring birth and $P_{a\times(s+id)}$ for the data with parental natal dispersal status (Table 2). Detection probability was always higher for females compared to males and for philopatric compared to dispersing individuals (Fig. 2). In addition, detection probability increases with age for dispersing individuals, while it is constantly high for philopatric individuals (Fig. 2).

Restricted recruit datasets testing for the effect of sibling non-independence

For all 10 restricted data subsets including only one recruit randomly selected for nests having recruited several siblings, the same model as for the full recruit data, i.e., $S_{a(2,3)\times id}$ $T_{a(1)\times sdp\times opd+a(2,3)\times id+sdp/id\times s}$ $P_{s+a\times id}$ (with juvenile survival fixed to 1), was selected, although the model with no effect of the dispersal status of the opposite-sex parent on the first transition probability was also retained. This strongly suggested that the non-independence of sibling recruits in the full data did not influence model selection and therefore was not a major issue here.

Differences in estimates obtained via the different models

As expected, heritability levels were lower when estimated using animal models compared to parent–offspring regressions, with a reduction of 30% for global dispersal heritability and 17% for natal dispersal heritability. However, heritability always remained significant. Furthermore, in all cases, offspring dispersal probability was lower when estimated via CMR models compared to parent–offspring regressions, for both sexes and both parental dispersal status (Fig. 1). Offspring dispersal probability varied between 0.51 and 0.91 for females and 0.40 and 0.80 for males when estimated via parent–offspring regressions,

Table 2 CMR models selected for the full recruit data with parental dispersal status in the year of offspring birth and parental natal dispersal status

S	*T*	*P*	QAICc	Δ QAICc	NP	Deviance
Parental dispersal status in the year of offspring birth						
$a(2,3) \times id$	$a(1) \times sdp + a(2,3) \times id + sdp/id \times s + sdp \times opd$	$s + a \times id$	3,575.67	0.00	22	11,265.17
$a(2,3) \times id$	$a(1) \times sdp \times opd + a(2,3) \times id + sdp/id \times s$	$s + a \times id$	3,576.44	0.77	22	11,267.64
$a(2,3) \times id$	$a(1) \times sdp + a(2,3) \times id + sdp/id \times s + sdp \times opd$	$a \times [s + id]$	3,577.26	1.59	24	11,257.34
$a(2,3) \times id$	$a(1) \times sdp + a(2,3) \times id + sdp/id \times s + sdp \times opd$	$s + a \times id$	3,577.47	1.80	23	11,264.47
$[a(2,3) \times id] + s$	$a(1) \times sdp + a(2,3) \times id + sdp/id \times s + sdp \times opd$	$s + a \times id$	3,577.59	1.92	23	11,284.83
$a(2,3) \times id$	$a(1) \times sdp + a(2,3) \times id + sdp/id \times s$	$s + a \times id$	3,577.81	2.14	20	11,284.89
Parental natal dispersal status						
$a(2,3) \times id$	$a(1) \times sdp + a(2,3) \times id + sdp/id \times s$	$a \times [s + id]$	2,507.01	0.00	25	4,740.42
$a(2,3) \times id$	$a(1) \times sdp + a(2,3) \times id + sdp/id \times s$	$a \times id$	2,507.29	0.28	22	4,752.90
$a(2,3) \times id$	$a(1) \times sdp + a(2,3) \times id + sdp/id \times s + sdp \times opd$	$a \times [s + id]$	2,508.74	1.73	27	4,735.77
$a(2,3) \times id$	$a(1) \times sdp + a(2,3) \times id + sdp/id \times s$	$id \times [s + a]$	2,508.80	1.79	22	4,755.79
$a(2,3) \times id$	$a(1) \times sdp + a(2,3) \times id + sdp/id \times s + sdp \times opd$	$a \times id$	2,508.81	1.80	24	4,747.87
$a(2,3) \times id$	$a(1) \times sdp + a(2,3) \times id + sdp/id \times s$	$s + a \times id$	2,508.96	1.95	20	4,764.05
$a(2,3) \times id$	$a(1) \times sdp \times opd + a(2,3) \times id + sdp/id \times s$	$a \times [s + id]$	2,510.21	3.20	27	4,738.61

In both cases, the models presented are those with QAICc of less than two units difference with the best model, plus the next model. Survival (*S*), transition (*T*) and capture (*P*) probabilities depending on age (*a*, differentiating 1, 2 and 3 or more years old individuals), sex (*s*), individual dispersal status (*id*) and parental dispersal status (same-sex parent: *sdp*, opposite-sex parent: *odp*). *Δ QAICc* difference between the QAICc values of the model considered and the best model, *NP* number of parameters. Note that juvenile survival $S_{a(1)}$ is fixed to 1 here since we considered only recruits, i.e., individuals that survived at least up to age 1. See text for further details

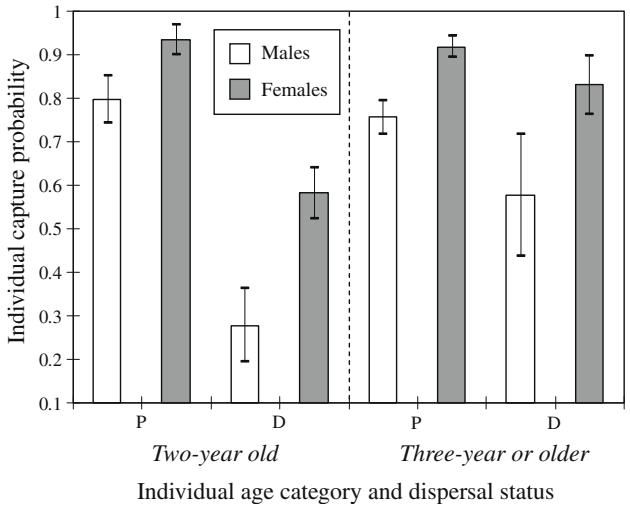

Fig. 2 Individual capture probability (±1 SE) according to sex, age and dispersal status, for individuals aged 2 years or more. *D* Dispersing individual, *P* philopatric individual. Parameter estimates come from model $P_{s+a\times id}$ for capture probability on data with parental dispersal status in the year of offspring birth, after the first capture was deleted for all individuals. This was done in order to ensure valid GOF tests and precise parameter estimates since the capture probability of some yearling categories appeared to be non-estimable in CMR models on full recruit data. No capture probability was therefore estimated here for yearlings

and between 0.37 and 0.62 for females and 0.27 and 0.44 for males when estimated via CMR models on full recruit data. Depending on sex and parental dispersal status (natal dispersal or dispersal in the year of offspring birth), offspring dispersal probability was reduced by 33–45% in CMR models (Fig. 1). However, and more importantly, the increase in offspring dispersal probability for a dispersing compared to a philopatric pair was similar for parent–offspring regressions (1.52 and 1.41 for males and females, respectively) and CMR models (1.51 and 1.50 for males and females, respectively), for the data with parental dispersal status in the year of offspring birth. It was slightly reduced for the data with parental natal dispersal (parent–offspring regressions: 1.83 and 1.79; CMR: 1.53 and 1.52, for males and females, respectively). In other words, accounting for imperfect detection probability did not change the observed pattern of parent–offspring resemblance in dispersal probability.

Discussion

Estimates of parent–offspring resemblance and heritability of dispersal probability

All three methods used here showed significant parent–offspring resemblance and/or heritability of between-patch dispersal propensity in our Collared Flycatcher population. Offspring of dispersing parents were more likely to disperse than offspring of philopatric parents. Comparisons of dispersal status of genetically unrelated individuals sharing similar small-scale environmental conditions (offspring and neighboring breeders) using simple regressions suggested that genetic (and/or parental) effects explain a significant part of the observed parent–offspring resemblance (Doligez et al. 2009). This was confirmed by animal models. Taking into account imperfect individual detection with capture–recapture models (Lebreton et al. 1992) did not change the main results obtained here from quantitative genetic models, even though individual detection probability appeared both sensibly lower than 1 and heterogeneous between individuals depending on dispersal status, sex and age. Dispersing individuals were indeed always less likely to be detected/captured compared to philopatric ones. Whether this lower detection probability is due to lower mating and/or breeding success (Pärt 1991, 1994) or temporary dispersal out of the study area (Doligez et al. 1999; Doligez and Pärt 2008; Pärt and Gustafsson 1989) needs to be investigated. Contrary to previous examples mainly addressing survival rates (Gimenez et al. 2008; Martin et al. 1995; Schmidt et al. 2002), we therefore did not observe a major change in parent–offspring resemblance levels or patterns when accounting for imperfect detection probability.

Nevertheless, we obtained different estimates using different approaches. The heritability estimates given by animal models were, as expected, lower than the estimates given by classical parent–offspring regressions. A decrease of 5–50% is usually observed in heritability values for animal models compared to parent–offspring regressions (review in Kruuk 2004; see, e.g., MacColl and Hatchwell 2003; Réale et al. 1999 for examples of comparisons of estimates between parent–offspring regressions and animal models). The decrease observed here (30 or 17%) lies within this interval. Estimates of dispersal heritability using both parent–offspring regressions and animal models in the same population (but over different time periods) have so far been obtained for only one population (Greenwood et al. 1979; McCleery et al. 2004). For this Great Tit *Parus major* population, estimates were very similar for females but differed strongly for males (females: 0.24 ± 0.10 and 0.25 ± 0.06; males: 0.50 ± 0.15 and 0.25 ± 0.06, with parent–offspring regressions and animal models, respectively). However, these studies were based on dispersal distance that may be subject to biases due to spatial constraints and spatial heterogeneity of observing long-distance dispersal movements (see Doligez and Pärt 2008; van Noordwijk 1984). For the sake of simplicity when comparing methods, maternal and environment effects have not been considered here. Because these effects have been shown to strongly affect individual dispersal decisions in

this and other populations (e.g., Doligez et al. 2004; Tschirren et al. 2007), further work is needed to separate additive genetic from other sources of phenotypic variation in dispersal using animal models (Kruuk and Hadfield 2007). The levels of parent–offspring resemblance in dispersal were similar when estimated using parent–offspring regressions and CMR models, but the estimated offspring dispersal probability was notably lower with CMR models. The reason for this lower offspring dispersal probability is unclear and needs further investigation.

Ignoring imperfect individual detection may be expected to lead to biased estimates of parent–offspring resemblance if detection probability depends not only on the dispersal status of the individual but also of its parents. In other words, only complex patterns of detection heterogeneity among individuals, involving memory effects, may bias estimates of parent–offspring resemblance. Such situations are likely to occur because dispersal often represents a single behavioral response to many potential selective pressures in a given population (Clobert et al. 2001, 2008; Dobson and Jones 1985). For instance, offspring dispersal may simultaneously be a response to local competition for offspring of dispersing parents if parental dispersal is triggered by lower competitiveness and a response to the risk of inbreeding for offspring of philopatric parents. This could lead to different dispersal modes, thus different detection probability for dispersing offspring depending on parental dispersal status. Ultimately, this could bias resemblance estimates since fewer dispersing offspring would be detected for either dispersing or philopatric parents. The absence of a clear bias in the present example does not preclude such an influence of imperfect individual detection on patterns of parent–offspring resemblance in dispersal since our CMR models did not test for the influence of parental dispersal status on offspring capture probability. In order to test for such effects, memory models in which capture probability depends on both current and previous state, i.e., here parental dispersal status at age 0, should be implemented (Brownie et al. 1993; see also Pradel et al. 2003).

Each method used here allowed us to account for a specificity of the data when estimating heritability of dispersal probability or parent–offspring resemblance but ignored other issues. First, parent–offspring regressions do not easily allow discriminating between genetic and environmental effects in natural populations (i.e., uncontrolled environments) (Kruuk 2004, 2008). Second, reliable estimates using animal models require knowledge of parentage relationships over a large number of generations (i.e., a good pedigree depth). Because animal models use the full parentage relationship information, they are, however, more powerful when they can be used than both parent–offspring regressions and our CMR approach, which use only the restricted direct links between parents and offspring. Third, neither parent–offspring regressions nor animal models can account for imperfect detection of individuals in the wild, which can lead to flawed biological inferences (Gimenez et al. 2008; Martin et al. 1995). Finally, classical CMR software do currently not account for random effects such as genetic and family effects (e.g., non-independence of siblings or same parents in different breeding events), although the incorporation of genetic random effects in CMR models has very recently been undertaken and is thus starting to become available (Papaïx et al. 2010). Computing heritability estimates of discrete traits using multi-state CMR models will be particularly relevant to compare with estimates obtained using quantitative genetic approaches (see also below).

State uncertainty: the particular case of dispersal

An additional difficulty arises when defining individual state requires comparing two successive observations of the individual. This is the case here with dispersal status, defined by comparing the successive breeding locations where the individual is captured. By construction, this leads to individual state uncertainty following non-detection (which also applies to parental dispersal status). When an individual is not caught, its subsequent dispersal status may be misassigned depending on whether the individual bred and stayed in the same patch or changed patch during the year when it was not detected, and stayed or changed patch again in the subsequent year (see Appendix). Recent CMR multi-event models take into account state uncertainty by incorporating probabilities of assigning a given state to a given observed event (Pradel 2005). However, these methods address one-step processes in which uncertainty is associated to the observation itself, i.e., without temporal delay. Here, uncertainty is linked to imperfect detection in the previous capture occasion rather than being intrinsically linked to direct observations, and thus has a somewhat different structural origin. In other words, individual dispersal state will be known with certainty when an individual is observed in two successive years, but the same state will be uncertain when the individual is not detected in the previous year(s). Therefore, applying multi-event models to address this type of uncertainty may require including memory effects, which may not be straightforward.

Including non-recruited young: data non-independence and unknown sex

Because dispersing individuals have a lower detection probability than philopatric individuals at all ages, including non-recruited fledglings in the data could be expected to increase the overall estimated offspring dispersal probabilities in CMR models, and thus reduce the

observed differences between parent–offspring regressions and CMR models. However, to what extent this change would affect the influence of parental dispersal status on offspring dispersal probability (i.e., the first transition probability), that is, the estimated level of parent–offspring resemblance in dispersal probability, needs to be investigated. Two main problems arise when considering non-recruited fledglings: (1) non-independence of siblings and (2) unknown sex of non-recruited individuals. The results obtained here on restricted recruit data suggest that sibling non-independence may not strongly affect model selection or parameter estimates. However, including non-recruited fledglings will considerably increase the level of data non-independence since nests fledged on average 3–4 young per nest (range 1–9; Doncaster et al. 1997). Because family effects cannot be included as random effects in current CMR models, an indirect approach by randomly selecting one fledged young per family may in that case also be needed to investigate the effect of data structure on GOF tests and model selection. Such an approach should, however, strongly decrease the power of analyses since juvenile survival is close to 15% (Doncaster et al. 1997).

The unknown sex of non-recruited fledglings poses problem because dispersal is sex-biased in this population as in many other bird populations (Greenwood and Harvey 1982; Paradis et al. 1998), and sex may also interact with dispersal status on detection and future dispersal probability. Because only sex-specific numbers of recruits are known, sex-specific juvenile survival and capture probabilities cannot be obtained by modeling uncertainty on fledgling sex using multi-event models due to parameter identifiability problems. Again, fledgling sex could be taken into account using indirect approaches, for instance by randomly attributing sex to each non-recruited fledgling according to observed fledging sex ratio in the population (which is known for a subset of nests; Ellegren et al. 1996; Sheldon and Ellegren 1996) and running model selection on repetitions of simulated data.

The need for non-biased heritability estimates with "capture–recapture animal models"

Based on the comparison of currently available quantitative genetic and capture–recapture methods, it is difficult and at best indirect to conclude that imperfect and heterogeneous individual detection probability does not affect the estimation of dispersal propensity heritability in our population. To predict evolutionary responses to environmental changes in terms of dispersal, it is, however, crucial to obtain unbiased heritability estimates of realised dispersal events in natural populations over sufficiently large spatial and temporal scales. This can prove difficult because of the need to track an unbiased sample of parent and offspring movements under frequent imperfect individual detection (Doligez and Pärt 2008; Kokko and López-Sepulcre 2006; van Noordwijk 1984). A statistical framework combining quantitative genetic and multi-state capture–recapture approaches into "capture–recapture animal models" (O'Hara et al. 2008; Papaïx et al. 2010) is still needed to estimate heritability of discrete traits while accounting for imperfect detection in the wild. The incorporation of random effects into capture–recapture models has recently been initiated using state-space model formulation (Royle 2008), especially in the context of estimating survival heritability (Papaïx et al. 2010). We expect this integration of random effects to be one of the main developments of multi-state CMR models in the near future, allowing in particular the unbiased estimation of heritability of many life-history and behavioral traits.

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Appendix 1: Map of the study area and choice of between-patch dispersal probability as the variable of interest

Figure 3 shows the spatial configuration of the study site, which comprises 14 spatially discrete forest patches of varying size, in which nest boxes have been provided for breeding flycatchers. The patches are separated by >100 m of habitat unsuitable for breeding. Dispersal was defined here as a change of patch between successive years. We preferred this binary definition of dispersal (dispersal versus philopatry) over dispersal distance because distance was likely to be strongly constrained by the spatial configuration of our study area. In particular, when dispersal distance is used to compute heritability estimates (e.g., McCleery et al. 2004; Pasinelli et al. 2004), constraints linked to the spatial configuration of the study area may lead to biased estimates as soon as true (rather than observed) dispersal distance in the population is large compared to the size of the study area (see Doligez and Pärt 2008). Estimates of dispersal distance heritability may indeed be inflated by spatial heterogeneity in detecting long-distance dispersal events within the study area such that offspring dispersing longer distances are more likely to

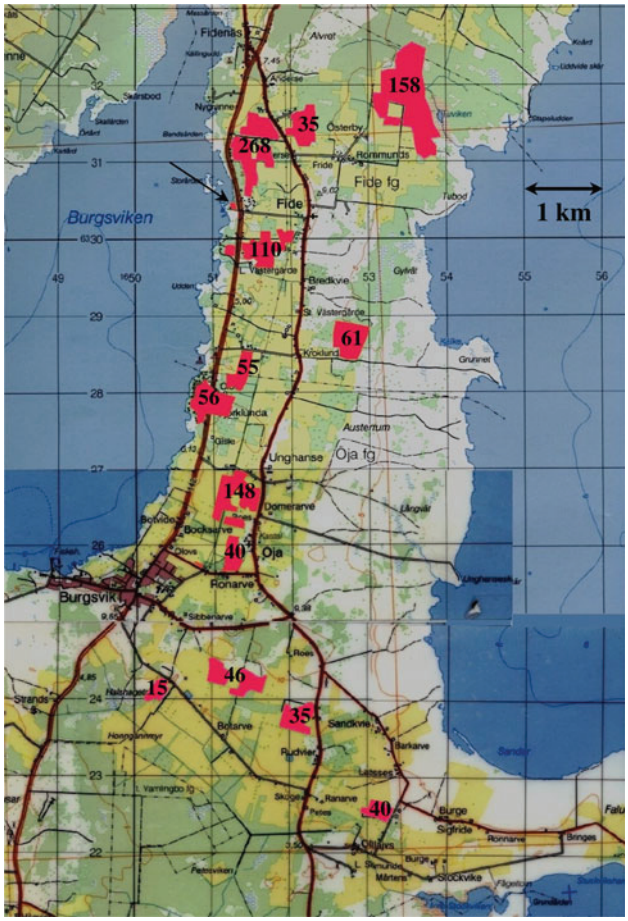


Fig. 3 The study area. The 14 breeding patches are shown in *red*, with the average number of boxes per patch (the smallest patch, comprising only a few nest boxes, is indicated by an *arrow*)

be detected for parents having themselves dispersed long distances within the area (as discussed in the case of the Great Tit *Parus major*; Greenwood et al. 1979; van Noordwijk 1984). Conversely, in our unsaturated population, individual emigration and immigration decisions at the patch scale should be relatively unconstrained. See Doligez et al. 2009 for more discussion.

Over the 26 years of the study, we obtained data from 999 nests where the dispersal status of both parents in the year of offspring birth was known compared with 403 for which the natal dispersal status of both parents was known, corresponding to 1,404 and 576, repectively, local recruits.

See Fig. 3.

Appendix 2: Causes of individual non-capture in the study population and the issue of misclassifying individuals

In our Collared Flycatcher study population, adult capture was tightly linked to sex, breeding status and success. Adults could be missed for at least three different reasons.

1. A fraction of adults breeding in nest boxes was missed each year because of early breeding failure (on average 7.1 and 27.4% of breeding females and males are missed, respectively; Doligez et al. 2004). The fraction of missed individuals was lower for females than males because females were caught early during the breeding cycle (during incubation) while males were caught later (when feeding young).
2. An unknown, but potentially high (up to 15–20%; Gustafsson and Pärt 1990), fraction of adults did not breed each year. In this facultatively polygynous species, approximately 10% of males were estimated to attract a secondary female (Gustafsson 1989), thus leaving some males with no mate. The fraction of non-breeding individuals seemed, however, also high in females, and this may in part be due to higher success obtained when delaying breeding is compared to when starting breeding at age 1 (Gustafsson and Pärt 1990; Sendecka 2007).
3. Some individuals may have temporarily emigrated out of the study area or bred in natural holes (whose availability was highly variable among years and patches) or boxes in gardens, which were less accessible.

As a result, non-capture events were frequent in the population (see text). Because individual dispersal status was defined by comparing current to previous location, there was a risk of misclassifying individuals when they were not caught in the year before, depending on the reason for missing them. If individuals were missed because they did not breed, we considered that their dispersal status was not defined in the year when they were missed and therefore their subsequent location defined their dispersal status without ambiguity (Table 3). However, when individuals bred in the year when they were missed, their dispersal status may have been misassigned depending on their breeding location in the year preceding and following the non-capture. There were two cases of misclassification (Table 3). First, apparently non-dispersing individuals (i.e., breeding in patch A in years t and $t + 2$) may in fact have been dispersing individuals if they bred in another patch (B) in year $t + 1$. Second, apparently dispersing individuals (i.e., breeding in patch A in year t and in patch B in year $t + 2$) may in fact have been non-dispersing individuals if they had already dispersed to patch B in year $t + 1$ where they were missed. In all other cases, missed individuals were correctly classified (Table 3).

It is difficult to assess the relative importance and impact of such misclassification. In particular, the percentage of non-capture due to non-breeding was unknown, although it could have reached up to 15–20% (Gustafsson and Pärt 1990). Nevertheless, in this population as in many

Table 3 Potential cases of misassignment of individual dispersal status in the study population when comparing individual's breeding patch in years t and $t + 2$, i.e., following a non-capture event in year $t + 1$

Year t	Year $t + 1$ (non-capture event)	Year $t + 2$	Assigned status	Misclassification?
A	–	A	Non-dispersing	No
A	*A*	A	Non-dispersing	No
A	*B*	A	Non-dispersing	Yes
A	–	B	Dispersing	No
A	*A*	B	Dispersing	No
A	*B*	B	Dispersing	Yes
A	*C*	B	Dispersing	No

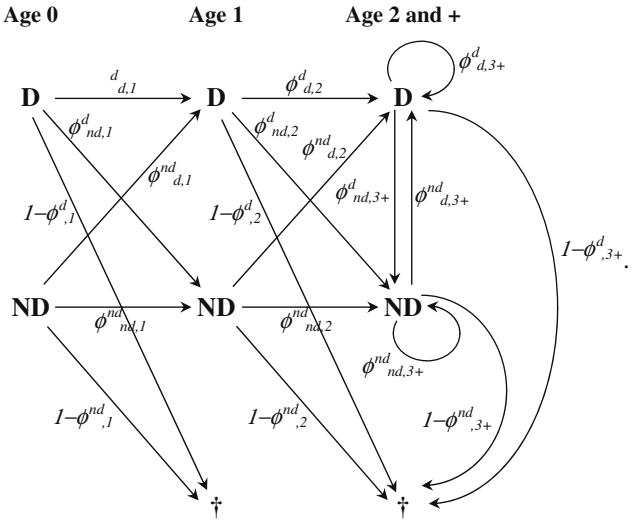
A and *B* are breeding patches of the study area, – represents individuals that did not breed. These examples are presented in the case when individuals were missed during one year, but the same reasoning applies when individuals were missed during several years in a row

others (Switzer 1993), reproductive success was one of the main determinants of individual dispersal decisions (Doligez et al. 1999; Pärt and Gustafsson 1989), while simultaneously affecting capture probability. Failed individuals were both more likely to disperse following failure and less likely to be caught during the year of failure. If we assume that most breeding individuals were missed because of reproductive failure (i.e., if we neglect temporary emigrants and individuals breeding in natural holes and garden boxes within the study area), misclassification should therefore mostly relate to the case when individuals returned to their previous breeding patch after a breeding failure in another patch (third case in Table 3). Individuals should indeed have a relatively low probability to stay in their new patch after a failure (sixth case in Table 3).

Unfortunately, there is, however, no way to discriminate between these situations or reliably assess their relative importance with the current data. In order to explore the potential impact of such individual dispersal status misassignment, detailed movement data should be obtained on non-breeding and failed individuals. This may require the use of radio-tracking devices in the field. Alternatively, simulation approaches could be used to explore different scenarios and assess the impact of different rates of misclassification on parameter estimates.

Appendix 3: Diagram of the capture–recapture models used to estimate parent–offspring resemblance in dispersal behavior

The three states in the multi-event capture–recapture models (Pradel 2005) used here were: disperser (D), non-disperser (ND) and dead (†). The first state of the capture history (initial state, age 0) corresponded to parental dispersal status since dispersal status could not be defined for juveniles (only recruits with parents of known dispersal status were included in the analysis; see text). The graph shows the transition parameters ϕ combining survival and transitions between dispersing states D and ND for the three age classes considered (survival and transitions between dispersing states were modelled separately in E-SURGE; Choquet et al. 2009). Note that $\phi^X_a = \phi^X_{D,a} + \phi^X_{ND,a}$, where X is the initial dispersal status, D and ND are the arrival dispersal status, and a is the age class. The parameters testing the existence of parent–offspring resemblance in dispersal were therefore included in parameters $\phi^X_{D,1}$ and $\phi^X_{ND,1}$ (age 0 to 1): if resemblance occurred, we predicted that $\phi^D_{D,1} > \phi^{ND}_{D,1}$ and $\phi^D_{ND,1} < \phi^{ND}_{ND,1}$ (if survival did not differ depending on dispersal status)



Appendix 4: Choice of the 10 restricted recruit datasets used to test for the effect of sibling non-independence on CMR model selection

See Fig. 4.

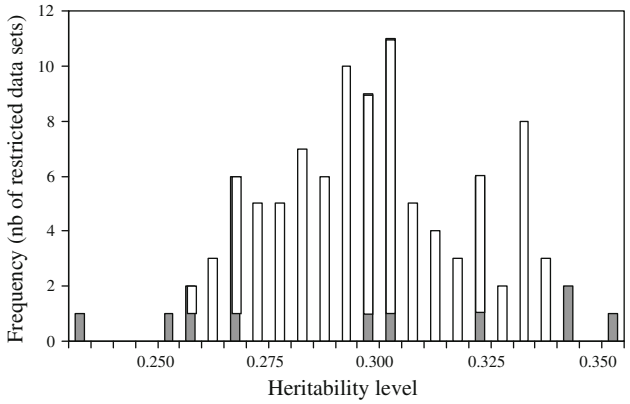


Fig. 4 Distribution of the 100 values of heritability obtained with parent–offspring regressions using restricted recruit datasets (with one randomly chosen recruit per nest) and (in *gray*) the 10 datasets chosen to test for the effect of non-independence of sibling recruits on CMR model selection and parameters estimates

Appendix 5: Estimates of parent–offspring resemblance in dispersal behavior: increase in offspring dispersal probability between philopatric and dispersing parents

See Table 4.

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Table 4 Percentages of increase in offspring between-patch dispersal probability from a philopatric to dispersing parent, depending on (1) offspring sex, (2) sex of the parent, (3) parental dispersal status considered (in the year of offspring birth or parental natal dispersal) and (4) dispersal status of the other parent (*D* dispersing, *P* philopatric)

Offspring sex	Parent	Method	Parental dispersal in the year of offspring birth		Parental natal dispersal	
			Other parent D	Other parent P	Other parent D	Other parent P
♂	Mother	P–O regr	43.5	26.2	64.2	8.8
		CR	20.2	9.3	48.8	32.7
	Father	P–O regr	45.3	27.7	39.6	−7.5
		CR	39.9	27.3	13.8	1.5
♀	Mother	P–O regr	38.1	66.1	18.4	14.1
		CR	40.8	32.1	19.6	12.8
	Father	P–O regr	7.9	29.7	23.6	19.1
		CR	15.1	8.0	33.4	25.8

Percentages of increase are computed as $(d_D - d_P)/d_P \times 100$, where d_X is the offspring dispersal probability for the considered parent of dispersing status X (X = D or P), estimated using parent–offspring regressions (P–O regr) and capture–recapture models (CR). The negative value indicates a decrease in offspring dispersal probability

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